BULLETIN OF THE RESEARCH COUNCIL OF ISRAEL

Section D BOTANY

Bull. Res. Counc. of Israel. D. Bot.

Continuing the activities of the Palestine Journal of Botany, Jerusalem and Rehovot Series

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1 A revision of the genus Retama Boiss.

M. Zohary

- Distribution patterns of diploid and tetraploid forms of \overline{D} a ctylis glomerata L. in Israel U. Nur and D. Zohary
- 23 Xylem structure and annual rhythm of development in trees and shrubs of the desert. II. A cacia tortilis and A. raddiana

 A. Fabn
- 29 Citrus germination and emergence as influenced by temperature and seed treatments

 S. P. Monselise
- 35 Causes of rapid wilting of cut dahlias and means to improve their keeping qualities

 Pnina Bar-Sella
- 39 Bacterial soft rot of avocado fruit. II. Zafrira Volcani
- 44 Endurance of a drought period beyond the wilting point

 Y. Waisel

NOTES:

- The calcium and magnesium content of germinating lettuce seeds

 Y. Ben Shaul
- 51 Native types of Oryzopsis miliacea (L.) Asch. et Schw. in Israel Z. Nahve
- 53 Growth and development of lettuce germinated in gibberellic acid

 Alexandra Poljakoff-Mayber and A. M. Mayer

BULLETIN

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193 V.7D-°D

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Page

- 1 A revision of the genus Retama Boiss. M. Zohary
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A REVISION OF THE GENUS RETAMA BOISS.

M. ZOHARY Department of Botany, The Hebrew University of Jerusalem

Retama is a small genus, very close to Genista and Spartium and confined to the Mediterranean and the Saharo-Sindian regions. The name stems from the biblical "rotem", later modified by the Arabs into "retam". It was first applied as an epithet (Genista raetam) by Forskal (Fl. aeg.-arab. Cent. VIII, p. 214, 1775) and later used as a generic name by Raffinesque (Sylva Tellureanum p. 22, 1838) for the two Linnean species of Spartium, viz. Sp. monospermum and Sp. sphaerocarpum. This transfer is, however, invalid, because the author did not retain the Linnean epithets for the above species. Boissier (Voy. bot. Esp. 2, p. 143, 1839), who applied this name again, based the genus Retama on the two above mentioned Linnean species of Spartium, retaining their original epithets. He also described the genus and gave sufficient reasons for its separation from allied genera.

Webb (Phytogr. canar. Sect. 2, p. 54, 1842) added to the two known species a new binomial from the Canary Islands. The first to monograph this genus was Spach (Ann. Sci. nat. 2 Sér., 19, 1843) who transferred it back to Spartium and added a few new binomials, excluding R. sphaerocarpa from it. Not agreeing with this transfer, Webb (Ann. Sci. nat. 2 Sér., 20, 1844) criticised Spach and advocated the retention of Retama as a separate genus. He did not accept some of Spach's binomials, but in a later article (Otia hispanica, ed. 2, 1853) described two more

species and reestablished one species previously discarded by him.

While some authorities, e.g. De Candolle (in Prodr. 2, 1825), Bentham and Hooker f. (Gen. 1, 2, 1865), Taubert (in Engler und Prantl, Natürl. Pflanzenfam. 3, 1894), the authors of Index Kewensis, included the genus within Genista, other authorities well acquainted with this genus, e.g. Boissier (Fl. or. 2, 1872), Willkomm et Lange (Prodr. Fl. hisp. 3, 1880), Jahandiez et Maire (Cat. Pl. Maroc 2, 1932) and many others, have kept Retama as a distinct genus. The present author also supports this view. A detailed examination of the relevant species in the Kew Herbarium, the Herbarium of the British Museum, that of the Muséum d'Histoire Naturelle, Paris, and of the Hebrew University, Jerusalem, has shown that many of the binomials hitherto described are based on very obscure, variable, or otherwise insignificant characters and should be reduced to varieties or fall into synonyms. Thus out of thirteen or more "species" referred to this genus, only four can be retained on the specific level.

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As there are only very few diagnostic characters for the specific distinction in this genus, and the parts needed are not always found in the herbarium specimens, the identification of the material was extremely difficult. Only by the use of a great number of specimens was it possible to gain an insight into the genus. No wonder, that the early students of this genus, who had very scant material at their disposal, were misled by its variability and established many species, especially on the basis of the exceedingly variable fruit forms.

The present author would have hardly undertaken to revise this small but very intricate genus, were it not for the difficulties he met in the identification of the many forms of *Retama* occurring in Palestine. According to the descriptions published, the local *Retama* forms would be classed under six different species, while as a result of the present revision the whole material of Palestine is included within a single species only.

The author is indebted to the Curator of the Kew Herbarium, the Herbarium of the British Museum (Natural History) and the Muséum d'Histoire Naturelle in Paris, for giving him the facilities or lending him material for study.

RETAMA Boiss., Voy. bot. Esp. 2:143 (1839).

Webb, Phytogr. canar. Sect. 2: 53 (1842); Ann. Sci. nat. 2 Sér., 20: 276 (1844); Otia hisp. ed. 2: 22 (1853). — Boelia Webb, Otia hisp. ed. 2: 20 (1853). — Genista Linn., Gen. Pl.: n. 859 (1737) p.p.; Lam., Enc. 2: 616 (1786) p.p.; Benth. et Hook. f., Gen. Pl. 1, pars 2: 482 (1865) p.p. — Spartium Tourn., Inst. 1: 644 (1719) p.p.; Linn., Sp. Pl.: 708 (1753) Spach, Ann. Sci. nat. 2 Sér., 19: 285 (1843).

Broom-like shrubs or small trees with erect, ascending or deflexed, sulcate and silky-hairy branches. Leaves small, short-lived, linear, lanceolate to ovate-oblong. Flowers white or yellow. Calyx urceolate-campanulate or turbinate, circumcisely caducous at base, rarely persistent, 2-lipped; upper lip with 2 triangular, ovate or lanceolate, acute lobes, lower lip 3-toothed. Corolla papilionaceous, claws of petals adherent to staminal tube; standard plicate, oblong, ovate to orbicular; wings lanceolate or oblong; keel ovate to oblong-lanceolate, generally shorter than wings. Stamens 10, monadelphous; anthers muticous to apiculate. Ovary sessile or short-stipitate, 2 - to many-ovuled; style filiform, incurved, glabrous; stigma papillose. Pod ovate, oblong, elliptical or globular, 1 - rarely 2-seeded, short apiculate or beaked, indehiscent or tardily incompletely dehiscent along ventral suture; epicarp thin, smooth or wrinkled, mesocarp fleshy, then dry or pulpous, endocarp membranaceous or parchment - like. Seeds yellow or brown to black, globular, ovate or somewhat kidney-shaped, with testa hard, thick and leathery. Radicle thick, incurved, less than half as long as incumbent cotyledons.

Key to the species

- 1. Pods and calyces densely hairy or tomentose. Morocco.
- R. dasycarpa Coss. - Pods glabrous
- 2. Flowers small, not exceeding 8 mm in length, corolla yellow. Portugal, Spain, Morocco, Algeria, Tunisia.

R. sphaerocarpa (L.) Boiss.

- Flowers larger, corolla white

3. Keel of corolla cuspidate. Pod cultriform or rhomboid-ovate, with a short mucro at top of ventral side. Portugal, Spain, Morocco.

R. monosperma (L.) Boiss.

- Keel of corolla obtuse, rarely acuminate. Pod not cultriform, Canary Islands, Morocco, Algeria, Tunisia, Tripolitania, Sicily, Egypt, Sinai, Saudi Arabia, Palestine, Lebanon.

R. raetam (Forsk.) Webb

1. Retama dasycarpa Coss.

Illustr. Fl. atl. 2: 25, t. 112 (1892; excl. ramis foliatis); emend. Maire, Bull. Soc. hist. nat. Afr. du Nord 13: 38 (1922); ibidem 29:413 (1938). — Genista das ycarpa Ball., Spicil. maroc., in J. Linn. Soc. London 16: 398 (1878; sine descriptione).

Erect shrub, branching from base. Branches terete, sulcate, pubescent or glabrescent. Leaves sparse, deciduous, simple, obovate or oblong, obtuse or retuse, silkyhairy. Flowers small, 5-6 mm long, in short, rather dense racemes with short, hairy pedicels. Calyx short-campanulate, circumcisely caducous, 2-lipped; lower lip 2-lobed, as long as ovate, obtuse, almost entire upper lip. Corolla yellow, villouspubescent; standard almost orbicular, retuse, as long as wings and keel. Pod densely woolly, compressed, subglobular, indehiscent, 9-10 mm long, 1 - 2-seeded. Seeds smooth, compressed, almost orbicular, yellow (Figure 1).

Selected specimens: MOROCCO: Djebel Afougueur, August 1873 Ibrahim (K lectotype!); High Atlas, Taddert Marakesh-Ouarzaalh Road, 1600 m, Mai 1937 J. Chaworth-Musters 153 very common (BM); Grand Atlas in Convalle fl., Ait Messane, ca. 1500 m, June 1926 H. Lindberg (K); between Tassgirh and Litmasan Atlas, Mai 1871 G. Maw (K).

Distribution: Morocco.

2. Retama sphaerocarpa (L.) Boiss. Erect, branching shrub, 60-90 cm high. Branches numerous, ascending or erect, thin, terete, sulcate, glabrous. Leaves deciduous, simple, filiform to linear-lanceolate, silky-pubescent. Flowers small, 6-8 mm in diam., in dense racemes with short, hairy pedicels. Calyx persistent or circumcisely caducous, about 3 mm long, pubescent or glabrous; lower lip 2-lobed, upper longer with three distinct elongated teeth. Corolla yellow, glabrous or sparsely pubescent; standard almost orbicular, obtuse, shorter than keel; wings lanceolate, somewhat shorter than keel. Pod indehiscent, ovate to globular, muticous or short-apiculate, 7-9 mm long; pericarp membranaceous, yellowish. Seeds kidney-shaped. -

Calyx persistent also in fruit.
 Calyx circumcisely caducous after anthesis.

var. sphaerocarpa var. atlantica (Pomel) Batt.

2a. R. sphaerocarpa (L.) Boiss. var. sphaerocarpa

R. sphaerocarpa (L.) Boiss., Voy. bot. Esp. 2: 144 (1839); Webb, Ann. Sci. nat. 2 Sér., 20: 282 (1844); Willk. et Lange, Prodr. Fl. hisp. 3: 419 (1880); Batt. et Trab., Fl. Alg. 1: 202 (1888-90); Bonn. et Barr., Cat. Pl. vasc. Tun.: 99 (1896); R. sphaerocarpa (L.) Boiss. var. eu-sphaerocarpa Maire, in Jah. et Maire, Cat. Pl. Maroc 2: 357 (1932); — Boelia sphaerocarpa Webb, Otia hisp. ed. 2: 21, t. 15 (1853). — Genista sphaerocarpos Lam., Enc. 2: 616 (1786); DC., in DC. Prodr. 2: 150 (1825). — Spartium sphaerocarpum L., Mant.: 571 (1767); Sp. sphaerocarpon Desf., Fl. atl.

2:129 (1800). — (Figure 2).

Selected specimens: PORTUGAL: Cintra, June 1933 S. C. Atchley 141 (K); Ajuda, June 1939 S. C. Atchley 100 (K). SPAIN: prope Sti. Laurenti el Escorial, October 1850 Herb. J. Gay (K), Matriti in collibus arenosis, June 1841 Reuter (K); Sierra Magina, Cambil, 800 m, June 1926 ex Herb. Cuatrecasas (K); Velez Rubio, June 1933 Ripley 114 (K); in collibus ap. Cartagenam, mai 1845 Funk (K); Andalusia, Sierra de la Pizarra, fl. June, fr. August 1888 Lange, Herb. E. Reverchon 201 (K); Almeria, Barranco de Caballar, 1830, Porta et Rigo 330 (K); Regnum Granatense in collibus, Malaga, Mai 1879 Porta et Rigo 957 (K). MOROCCO: S. Morocco, Shedma, fl. April, fr. May 1871 Hooker sub R. monosperma (K). ALGERIA: Kabylia Minor, Merouaha (Amoucha) in collibus copiose, 1865 E. G. Paris 44 (BM); Prov. Constantine, Plain de Batna, July 1853 Balansa 915 (K); Djebel Amour, 1860 Pomel (K); Algerian Sahara, Oued Nssa, zwischen Ghardia und Querrara (Guerrara), April 1914 E. Martert (BM).

2b. R. sphaerocarpa (L.) Boiss. var atlantica (Pomel) Batt. et Trab.

Fl. Alg. 1: 202 (1888-90); Jah. et Maire, Cat. Pl. Maroc 2: 357 (1932). — R. atlantica Pomel, Nouv. Mater. Fl. atl.: 172 (1874).

Selected specimens: MOROCCO: Montagnes du Sersou, du Nador à Goudjila, Kosni, Mai, sine anno, ex *Pomel* 1.c.); Moyen Atlas: Ouanizert, coteaux calcaires 1100 m, Mai 1927 E. Jahandiez 246 (K).

According to Jahandiez et Maire (1932), it occurs in Great Atlas, Demnat, 800-1400 m (Litardière et Maire) and in Bin-el-Ouidan (Jahandiez et Weiller).

Distribution of species: Portugal, Spain, Morocco, Algeria, Algerian Sahara.

R. sphaerocarpa reminds R. dasycarpa by its small yellow flowers, but its pods are glabrous. The persistence of the calyx is a more primitive character which has been retained only in var. sphaerocarpa of this species, while in var. atlantica, as in all other species of the genus, the calyx is shed by circumcision after anthesis. Var. atlantica can, thus, be regarded as a link between the otherwise isolated R. sphaerocarpa and the remaining species of the genus. An approximation to R. monosperma could be seen in the specimen from Shedma cited above, with larger pods and a broad ventral suture. Thus, there is no justification to establish for R. sphaerocarpa a particular genus Boelia as done by Webb. The author has not been able to examine var. mesogaea Webb (Otia hisp. ed. 2: 21, t. 16, 1853) with long acuminate calyx teeth.

3. Retama monosperma (L.) Boiss. Erect, divaricately branching shrub. Branches deeply sulcate. Leaves linear-lanceolate, obtuse, silky-hairy. Flowers

9-13 mm long, in loose racemes with short, hairy pedicels. Calyx urceolate or campanulate, circumcisely caducous, glabrous except for the often ciliate teeth, usually purple; upper lip with two triangular, acute or mucronate lobes, lower with three elongated, distinct teeth. Corolla white, hairy; standard rhomboid-ovate, somewhat shorter than obtuse wings, the latter as long as or shorter than the acuminate or cuspidate keel. Pods brown, somewhat compressed, cultriform-obovate, strongly gibbous at back, 12-16 mm long, 8-12 mm broad, with a short mucro bent toward the ventral suture; pericarp fleshy, thick, strongly wrinkled when dry, with a deep and straight ventral suture. Seeds almost kidney-shaped, brown or black.

1. Flowers 12-13 mm long; keel 10 mm long; teeth of lower calyx lobe long, linear, subulate. var. monosperma

 Flowers 9-11 mm long; keel 9 mm long; teeth of lower calyx lobe short, triangular.
 var. webbii (Spach) Maire

3a. R. monosperma (L.) Boiss. var. monosperma.

R. monosperma (L.) Boiss., Voy. bot. Esp. 2: 144 (1839); Webb, Phytogr. canar. Sect. 2: 56 (1842; exl. syn. Fontan.); Ann. Sci. nat. 2 Sér., 20: 278 (1844); Otia hisp. ed. 2: 25, t. 17 (1853); Willk. et Lange, Prodr. Fl. hisp. 3: 418 (1880). — R. monosperma (L.) Boiss. ssp. eu-monosperma Maire, in Jah. et Maire, Cat. Pl. Maroc 2: 357 (1932). — Genista monosperma Lam., Enc. 2: 616 (1786); DC. in DC., Prodr. 2: 150 (1825; excl. syn. Forsk.); Guss., Fl. sic. Prodr. 2: 363 (1828). — Spartium monospermum L., Sp. Pl.: 708 (1753); Desf., Fl. atl. 2: 130 (1800) p.p.; Curt. bot. Mag. 18: t. 683 (1803); Brot., Fl. lus. 2: 85 (1804). — Sp. clusii Spach, Ann. Sci. nat. 2 Sér., 19: 290, t. 16, fig. 3 (1843). — (Figure 3).

Selected specimens: PORTUGAL: Jagres (Tagres), 1939 T. Ogilire 24 (K); prope Setubal, Mai 1882 Matter 1952 (K); peninsula Troia (?), in arenosis ad oceanum, April 1848 C. Welwitsch, Herb. Hookerianum (K). SPAIN: Pinal de Plata près Puerto Santa Maria, fl. March, fr. Mai 1849 E. Bourgeau 133 (K); in arenosis maritimis juxta Gades, June 1851 J. Ball, sub R. clusii (K); in arenosis ad Linea, pr. Sinum Gibraltaricum, April 1895 Porta et Rigo 666 (K); Cataluna, Santa Codina, Pujobl, February 1920 J. Scioudair (K). MOROCCO: Tangier, sand dunes, April 1939 P. Davis 540 (K); Mogador, dans les sables, April 1867 B. Balansa (K); Agadir, fl. January, fr. February 1936 A. W. Trettewy (K).

3b. R. monosperma (L.) Boiss. var. webbii (Spach) Maire

In Jah. et Maire, Cat. Pl. Maroc 2:357 (1932). — R. monosperma Webb, Phytogranar. Sect. 2:56 (1842) p.p.; Ann. Sci. nat. 2 Sér., 20:278 (1844) p.p. — R. webii (Spach) Webb, Otia hisp. ed. 2:24 (1853). — Spartium webbii Spach, Ann. Sci. nat. 2 Sér., 19:291, t. 16, fig. 4 (1843). — (Figure 4).

Selected specimens: MOROCCO: Tangier, in arenis maritimis, April 1913 Pitara 761 (K); La Banda, above el Charco, June 1858 Lowe (K); in arenosis maritimis, ca El Araix, February, March 1930 Font Quer, sub. var. bovei (Spach) Pau (K);

Safi, January 1931 A. W. Trettewy (K).

Distribution of species: Portugal, Spain, Morocco.

This is a well defined species, distinct in flower and fruit form. The cuspidate-acuminate keel of the corolla and the cultriform-ovate or rhomboid fleshy fruit, with a short mucro at the end of broad ventral suture, are striking characteristics. Var. webbii differs from the type by its smaller flowers and generally more elongated

racemes. Maire in Jah. et Maire (l.c.) erroneously referred ssp. bovei to this species. The latter differs largely by its corolla and pods from R. monosperma and should be included within R. raetam.

- 4. Retama raetam (Forsk.) Webb. Erect or diffuse, much branching shrub. Branches ascending, deflexed or pendulous. Flowers 10-17 mm long, in short dense racemes, white. Calyx urceolate-campanulate, green, brown, purple or violet; upper lip with two broad-triangular lobes, the lower with short, often connivent, triangular or lanceolate teeth. Corolla white, sometimes turning cream-coloured after drying; standard ovate, entire or notched, purple-veined, about as long as or somewhat shorter or longer than wings, the latter generally longer than obtuse or acute, rarely acuminate, keel. Pod globular, ovate, elliptic, rhomboid, fusiform or oblong, 7-20 mm long, 5-9 mm broad, with a short, erect mucro or with an erect or curved beak; pericarp membranous, leathery or fleshy, with a thin ventral suture, indehiscent or tardily dehiscent. Seeds yellow, brown or black.
 - 1. Flowers large (15-17 mm), yellowish-cream when drying; standard ovateoblong, shorter than wings; limb of keel about 1/3 shorter than that of wings

- Flowers smaller; standard ovate or almost orbicular, as long as or longer

than wings

2. Pods globular or nearly so, abruptly short-apiculate at apex. Mediterranean North Africa. var. bovei (Spach) Zoh.

- Pods obovate-elliptical, tapering to a beak. Sicily.

var. gussonei (Webb) Zoh.

3 (1). Pericarp fleshy, shining, strongly wrinkled also in ripe pods, narrowly dehiscent at ventral suture; beak tapering or curved. Seeds yellow. Low, diffusely branching shrubs, with recurved or deflexed upper branches.

Coastal Plain of Palestine and Sinai.

— Pericarp leathery, horny or parchment-like, indehiscent. Seeds brown to black, rarely yellow. Mostly erect shrubs

 Flowers 10-11 mm long; wings about 1½ as long as acuminate keel. Pod almost globular with a short mucro. Seeds yellow. North African coast.

war. duriaei (Spach) Letourn.

Flowers generally larger; wings as long as or somewhat shorter than obtuse or acute keel. Pods conspicuously beaked or mucronate. Seeds brown or black, rarely yellow. From Canary Islands to Arabia.

var. raetam

2

3

4a. R. raetam (Forsk.) Webb var. raetam

R. raetam (Forsk.). Webb, Phytogr. canar. Sect. 2: 56 (1842); Ann. Sci. nat. 2 Sér., 20: 279 (1844); Otia hisp. ed. 2: 23 (1853); Boiss., Fl. or. 2:37 (1872); Jah. et Maire, Cat. Pl. Maroc 2: 357 (1932). — R. hipponensis Webb, Otia hisp. ed. 2: 25 (1853). — R. duriaei Boiss., Fl. or. Suppl.: 159 (1888) p.p. — R. duriaei (Spach) Webb var. phaeocalyx Coss., in Coss. et Kralik, Bull. Soc. bot. Fr. 4:131 (1857). — R. rhodorrhizoides Webb, Phytogr. canar. Sect. 2:54 (1842); Ann. Sci. nat. 2 Sér., 20: 281 (1844). — R. microcarpa (Spach) Webb, ibidem: 280. — R. spachii Webb, ibidem: 281. — R. recutita Webb in Bourgeau, Pl. can. exsicc., n. 806, ex Bolle, Engl. bot. Jahrb. 14: 236 (1892). — Genista raetam Forsk., Fl. aeg.-arab.: 214 (1775; excl.

loc. Rosetta). — G. rhodorizoides Webb, Phytogr. canar. Sect. 2: t. 48 (1836-50). — G. monosperma Del., Fl. Eg.: 21 (1813; excl. syn. L.); Fres., Mus. Senck. 1: 185 (1834; excl. syn. L.); Decaisne, Fl. sin., Ann. Sci. nat. 2 Sér., 3: 265 (1834); Lindl., Bot. Reg. 22, t. 1918 (1836); Link in Buch, Beschr. canar. Ins.: 156 (1825). — Spartium raetam (Webb) Spach, Ann. Sci. nat. 2 Sér., 19: 288, t. 16, fig. 1 (1843). — Sp. microcarpum Spach, ibidem: 292, t. 16, fig. 5. — Sp. rostratum Spach var. macrorhynchum (t. 16, fig. 6), var. podocarpum (t. 16, fig. 7) et var. microrhynchum (t. 16, figs. 1, 9) Spach, ibidem: 293. — Sp. semperflorens Spach, ibidem: 294, t. 16, fig. 10. — Sp. ambiguum Spach, ibidem: 295. — Sp. dubium Spach, ibidem: 295. — Sp. affine Spach, ibidem: 296. — (Figures 5, 6, 7, 8).

Selected specimens: CANARY ISLANDS: Palma, Barranco del Carmen, Mai 1913 T. A. Sprague et Hutchinson 145 (K); Teneriffa, La valle St. Jacobi, Febr. 1844, or 1868(?) Webb, Herb. J. Gay (K); Gran Canaria, Caldera de Bandama, April 1894 R. P. Numay 3675 (K); Lancerotta, Los Tanques, February 1846 E. Bourgeau 392 (K). MOROCCO: Sud-ouest de Maroc, Assaka, 1875 Mardochée (K); Ait Grizane, Cercle de Azilal vers l'oued el Abid, 800m, March 1923 sine collectore 63 (BM); Aglatben, Abd el Djebar in arenosis, April 1913 C. J. Pitard 3278 (K). ALGERIA: Oran, Sud de la Province d'Oran, Ravin du Khraneg el Melah à Macta, June 1856 Kralik (K); Alger, near Sidi Maklouf, S. of Djelfa, April 1947 A. H. G. Alston and N. D. Simpson 53 (BM); Alg. Sahara, El Golea, February 1931 R. Meinertzhagen 304 (K); Constantine, env. de Biskra, February 1851 Jamin 322 bis (BM); Touggourt, February 1830, Lynes (BM); Kabylia, embouchure du Saffsafa, Philippeville, Mai 1853 Gallerarand 913 (K). TUNISIA: Tabarca, sands and sandy fields, March 1930, A. Eig 46 (HUJ): Nefta, Mai 1889 Cosson (P); between Degache (Deguech) and Tozeur, March 1930 A. Eig 45 (HUJ); Gabès, February 1907 Pitard 76 (K). CYRENAICA: Tobruk, dune arenaire maritime, June 1912 Vaccari (FI). EGYPT: sine loco, 1762 Forskal 766 (CP, lectotype! specimen cum floribus solum); Earbin desert, betw. Cairo and Suez, March 1848 S. G. Cowper (K); Djebel Ataka prope Suez, February 1877 P. Letourneaux 40 (K); Mittlere aegyptische Wüste, Wad Lutt, sine dato G. Schweinfurth 83 (K). SINAI: Wadi Ghurundel to Wadi Kuseit, March 1882 Herb. G. Post (K); Wadi Hardon, fl. November 1883, fr. February 1884 H. C. Hart (K). SAUDI ARABIA: Wady Nejd, watershed, January 1947 D. Versey Fitzgerald 16674/2 (K). PALESTINE: Centr. Negev, Makhtesh Ramon, September 1953 M. Zohary and G. Orshan 713 (HUJ); Judaean Desert, Khirbeth Faziel, March 1946 D. Zohary 669 (HUJ); Jordan Valley, env. of Gesher Nehalim, rocks, Mai 1954 M. Zohary 662 (HUJ), Ein Gev, W. slope of Susita, rocks, February 1940, 621 (HUJ); Tel el Hammam, April 1886 G. Post (K); Gilead, rocky hills above Yabbok, 500 m, Mai 1911 Dinsmore and Meyers 507 (K).

4b. R. raetam (Forsk.) Webb var. gussonei (Webb) Zoh. comb. nov.

R. gussonei Webb, Ann. Sci. nat. 2 Sér., 20: 280 (1844); Otia hisp. ed. 2: 24 (1853); Guss., Fl. sic. Syn. 2, 2: 851 (1844). — R. duriaei Guss., ibidem, pars 1: 253. — Genista monosperma Guss., Fl. sic. Prodr. 2: 363 (1828; excl. syn.). — G. monosperma Lam. β gussonei Fiori, in Fiori et Paoletti, Fl. anal. d'Italia 2: 22 (1900). — (Figure 9).

Selected specimens: SICILY: De Licata a Spaccaforno, Mazarra, Maio, sine anno Gussone (K, lectotype!); in arenosis maritimis, Licata, 1882 Todaro 873 (K); sand hills between Licata and Terranova, March 1855 ex Herb. Stuart Mill (K); Terranova in arenis maritimis, Mai 1873 S. Sommier (K); sine loco, sine dato, Tenore sub Sp. monospermo (K).

This variety is well distinguished from all other *Retama* species by its large flowers (largest of the genus) and by its short keel (one third shorter than wings). It is also geographically isolated from other species by being confined to Sicily only.

4c. R. raetam (Forsk.) Webb var. bovei (Spach) Zoh. comb. nov.

R. bovei (Spach) Webb, Otia hisp. ed. 2: 24 (1853). — R. monosperma (L.) Boiss. β bovei (Spach) Webb, Ann. Sci nat. 2 Sér., 20: 279 (1844). — R. monosperma (L.) Boiss. ssp. bovei Maire, in Jah. et Maire, Cat. Pl. Maroc 2: 357 (1932). — Spar-

tium bovei Spach, Ann. Sci. nat. 2 Sér., 19: 297 (1843). — (Figure 10).

Selected specimens: ALGERIA: Oran, dans le littoral, Febr. 1869 Warian (K), Batterie espagnole, sables maritimes, fl. February, fr. April 1930 A. Faure (K), La Macta, in arenosis, 1850 Herb. G. Munby 93 (K), Mostaganem, dans les sables maritimes, fl. March, fr. June 1851 B. Balansa (K). Tunisia: in proscuris deserti prope Gabès, Mai 1884 L. Kralik 401 (BM). CYRENAICA: descent of Pass Bacur, betw. Barca and Tokva, April 1939 N. Y. Sandhill 2662 (K). EGYPT: in palmetis ad Mandara, prope Alexandriam, February 1878 A. Letourneaux 186, sub R. duriaei (K), entre Bab En (?) et Mandarah, March 1871 R. Oudarquy (K).

Webb (Otia hisp. l.c.) remarks that mature pods have not yet been seen from this variety and that he formerly had attached this taxon erroneously to R. monosperma. In fact it has nothing to do with R. monosperma and should be included within R. raetam. It is well distinguished by its large flowers, its linear, elongated teeth of the inferior calyx lobe, its obtuse keel. The flowers become cream-coloured after drying. Both in herbaria and in Floras it is often misnamed and confounded with R. duriaei, which itself is another variety of R. raetam, distinguished by its smaller flowers and its acute-acuminate keel as well as by its fruits (see later). Var. bovei occurs in Algeria, Tunisia, Cyrenaica and Egypt, while var. duriaei is probably confined to Algeria. Both are mainly coastal plants.

4c. R. raetam (Forsk.) Webb var. duriaei (Spach) Letourn.

Bull. Soc. bot. Fr. 36: 94 (1889). — R. duriaei (Spach) Webb, Ann. Sci. nat. 2 Sér., 20: 279 (1844); Otia hisp. ed. 2: 23 (1853); non Boiss., Fl. or. Suppl.: 159 (1888); Batt. et Trab., Fl. Alg. 1: 203 (1888-90); non Muschl., Man. Fl. Eg. 1: 473 (1912). — Spartium duriaei Spach, Ann. Sci. nat. 2 Sér., 19: 289, t. 16, fig. 2 (1843). — Sp. monospermum Desf., Fl. atl. 2: 130 (1800 quoad flores, excl. syn. et fructus descr.). — (Figure 11).

Selected specimens: ALGERIA: Dunes de La Calle, March 1843 Durieu? (K, lectotype!); de Bougie à la Calle, ex Batt. et Trab., Fl. Alg. 1, app. II, p. VIII, 1888-90).

Var. duriaei differs from the former variety by the short and acuminate keel of the smaller flowers. The pods are almost globular with a short straight central mucro. The mature fruits have membranous or coriaceous brittle pericarp; the seeds are yellow. This variety seems to intergrade with var. raetam and perhaps also with var. bovei for which it has been mistaken by many authors of the North African floras. It is doubtful whether var. duriaei, very accurately described by Spach (l.c.), occurs outside Algeria. The data on this variety recorded by Gauba, Engl. bot. Jahrb. 47: 286 (1935) and by Sickenberger, Contr. Fl. Eg.: 214 (1901) for Egypt should be referred to R. raetam var. bovei. Neither does var. duriaei occur in Palestine.

4d. R. raetam (Forsk.) Webb var. sarcocarpa Zoh. var. nov.

Legumen ellipticum vel ovatum vel subglobosum, subdehiscens, nitidum, etiam post maturitatem carnosum, diagonaliter et longitudinaliter valde rugosum, 10-20 mm longum; endocarpium saepe lanato-pulposum; rostrum rectum vel recurvum. Semina citrina, rarum viridia, ellipsoidea vel ovoidea vel subglobosa, 5-8 mm longa. — (Figure 12).

Pod elliptical or ovate or subglobose, subdehiscent, fleshy also after ripening,

strongly wrinkled, 10-20 mm long, often with woolly-pulpous endocarp; beak straight or recurved. Seeds lemon-yellow, rarely green, ellipsoid or ovoid or subglobose, 5-8 mm long.

Selected specimens: SINAI: Tih Desert, 45 km E. of Suez on the Suez-Bir Hassana road, May 1940 Zobary and Feinbrun 702; El-Arish, bank of wadi, Mai 1925 Eig 703. PALESTINE: W. Negev, env. of Gevulot, sand dunes, February 1957 Y. Waisel 532; N. Negev, Wadi Sekher (Wadi Mashash), sand dunes, May 1957 M. Zobary 507; Philistaean Plain, Ashqelon, sand dunes, Mai 1957 Y. Waisel 509 (type!), ibidem, env. of Wadi Faliq, sand dunes, March 1956 M. Zobary 508; Sharon Plain, Benei Beraq, April 1930 N. Naftolsky 506, ibidem, env. of Caesarea, sand dunes, June 1956 M. Zobary 501 (all in HUJ).

Distribution of species: Canary Islands, Morocco, Algeria, Tunisia, Tripolitania, Sicily, Cyrenaica, Egypt, Sinai, Saudi Arabia, Palestine, Lebanon.

R. raetam was described by Forskal (l.c.) as Genista raetam from a number of specimens collected in Egypt, in the environs of Rosetta (in northern Egypt) and between Cairo and Suez. The short diagnosis given by Forskal does not indicate whether it refers to the specimen from Rosetta or to that from Cairo-Suez. In the case of Rosetta, it is not improbable that the specimen in question is identical with var. bovei, while the specimens of Cairo-Suez would correspond to var. raetam. As only two specimens of the last-named locality are preserved in Forskal's Herbarium, one of them is proposed as a lectotype for R. raetam var. raetam.

This species is exceedingly variable in size and shape of the pods, in structure of the pericarp and also in flower characters. The five varieties distinguished here are based on more or less constant, easily recognizable characteristics. Var. raetam, which shows an array of intergrading, difficult to describe, fruit forms, includes not less than seven binomials that are discarded here for lack of discernible characters. As an example R. rhodorrhizoides may be mentioned, first described by Webb in Phytographia canariensis Sect. 2: 54 (1842) from material collected in the Canary Islands. Spach (l.c.) had split this species into six binomials, mainly on the basis of fruit form and other hardly perceivable characters. Later Webb, reviewing the genus (Ann. Sci. nat. 2 Sér., 20, 1844), reduced the number of the Canarian binomials to three, viz. R. rhodorrhizoides Webb, R. spachii Webb, R. microcarpa (Spach) Webb. However, one can hardly find any diagnostic characters either in the shape and size of the corolla parts or in the fruit, attributed to the Canarian binomials, which do not occur separately or combined in R. raetam var. raetam of Egypt and Israel. Consequently the author included the Canarian "species" within R. raetam.

The area of distribution of *R. raetam* is the largest in the genus. It comprises coastal Lebanon, Palestine, the Syrian Desert, Arabia, Sinai, Egypt, Cyrenaica, Tripolitania, Tunisia, Algeria, Morocco and the Canary Islands. This distribution pattern is shared by dozens of other species, viz. *Pistacia atlantica, Aerva tomentosa, Aizoon canariense, Gymnocarpos fruticosum, Notoceras canariense, Citrullus colocynthis, Francoenria crispa, Tricholaena teneriffae, Salvia aegyptiaca, Senecio flavus* and others. *R. raetam* is a Saharo-Sindian species with some well-defined ecotypes in the Mediterranean coastal plain of Africa and Israel, e.g. var. bovei, var. duriaei, var. sarcocarpa. Its occurrence in the Canary Islands suggests that the Saharo-Sindian variety has already existed during the Pliocene, before the separation of the Canary Islands from the African mainland. The Mediterranean representatives of this species may have been formed at a later date. This is especially plausible in view of the fact that the Coastal Plain of Israel, which comprises the main area of var. sarcocarpa, has not emerged from the sea before the Pleistocene.

PHYTOGEOGRAPHICAL CONCLUSIONS

The genus *Retama* is an offshoot of the ancient and widespread genus *Genista*. It shows a series of derived characteristics, e.g. simple and very short-lived leaves, monospermous indehiscent pods tending towards baccation, and a circumcisely caducous calyx.

The genus presumably originated and developed in north-western Africa, e.g. Morocco and Algeria, where all four species of the genus and most of its varieties are still concentrated. R. dasycarpa and R. sphaerocarpa seem to be the most ancient species. R. dasycarpa is endemic to the High Atlas of Morocco; R. sphaerocarpa also occurs in Spain and Portugal, and in one of its varieties an ancient character, namely the persistence of the calyx, is still preserved.

From this ancient group, notably from R. sphaerocarpa, the two other species could have developed in the following directions. R. monosperma has remained chiefly within the Mediterranean region along with R. sphaerocarpa. R. raetam, on the other hand, has occupied vast stretches of north-African and south-west Asian deserts, as well as of the southern and eastern Mediterranean coast. Along these coastal lands, four more or less distinct varieties, i.e. var. gussonei, var. bovei, var. duriaei and var. sarcocarpa, have found ecological niches, whereas the rather variable stock of var. raetam has remained within an area extending from the Canary Islands to the interior deserts of North Africa, Arabia and southern Palestine. As shown above, such a Saharo-Canarian distribution pattern is shared by many Saharo-Sindian plants.

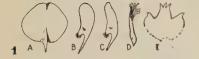


Figure 1

Retama dasycarpa Coss. (Morocco:
Dj. Afougueur).



Figure 2

R. sphaerocarpa (L.) Boiss. (Spain: Andalusia, Sierra de la Pizarra).

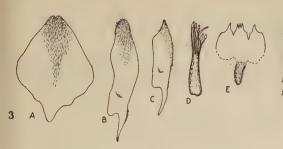


Figure 3

R. monosperma (L.) Boiss. var. monosperma (Portugal: peninsula Troia).

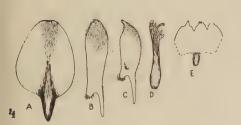


Figure 4

R. monosperma (L.) Boiss. var. webbii (Spach) Maire (Morocco: Tangier, ca El Araix, under var. bovei).

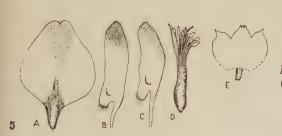


Figure 5

R. raetam (Forsk.) Webb var. raetam (Canary Isls.: Gran Canaria, under R. rhodorrhizoides).

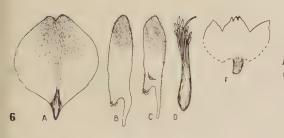


Figure 6

R. raetam (Forsk.) Webb var. raetam (Canary Isls.: Lancerotta, under R. microcarpa).

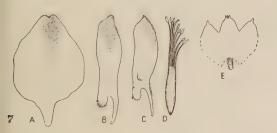


Figure 7

R. raetam (Forsk.) Webb var. raetam (Egypt: Earbin Desert).

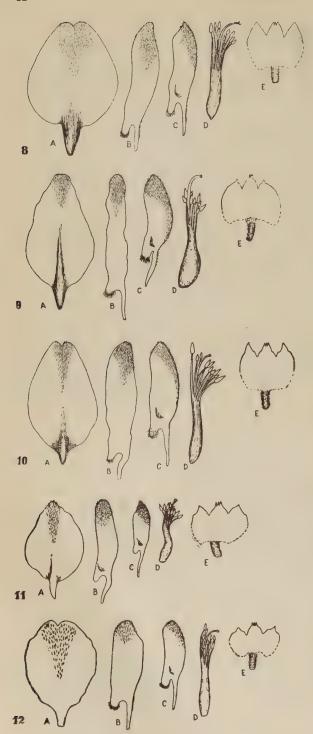


Figure 8

R. raetam (Forsk.) Webb var.
raetam (Palestine: Jordan Valley, Gesher).

Figure 9

R. raetam (Forsk.) Webb var.
gussonei (Webb) Zoh. (Sicily:
Terranova, under R. duriaei).

Figure 10

R. raetam (Forsk.) Webb var.
bovei (Spach) Zoh. (Algeria:
Oran, Mostaganem).

Figure 11

R. raetam (Forsk.) Webb var.
duriaei (Spach) Letourn. (Algeria
Dunes de La Calle).

Figure 12

R. raetam (Forsk.) Webb var.
sarcocarpa Zoh. (Palestine:
Philistaean Plain, Ashqelon).

DISTRIBUTION PATTERNS OF DIPLOID AND TETRAPLOID FORMS OF DACTYLIS GLOMERATA L. IN ISRAEL*

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ABSTRACT

Cytogeographical survey of *Dactylis glomerata* from about 150 stations in Israel reveals that diploid populations occur in the areas of Jerusalem, Nazareth and the Upper Galilee. They occupy only typical Mediterranean habitats and are confined to relatively small islands within the tetraploid territory. Tetraploids occupy a much wider range of habitats and are spread over most of the Mediterranean region of Israel and some of the semi-steppe border zone.

In Upper Galilee, and particularly in the Safad area, intricate distribution mo-

saics of the two chromosomal forms were found.

Contacts between diploids and tetraploids are common, and transitional zones

were found to be strikingly narrow.

In areas where both diploids and tetraploids occur, elevation, bed-rock and exposure have been recognized as the main ecological factors determining their distribution. However, in different areas the relative importance of these factors varies.

INTRODUCTION

Dactylis glomerata is a perennial grass common to central and northern Israel. Previous studies (D. Zohary 1956, Stebbins and D. Zohary 1958) have established the polytypic group of Dactylis glomerata L. as a large single polyploid complex. This complex contains at least eleven distinct diploid subspecies, each with restricted geographical distribution, as well as a large continuous tetraploid superstructure which is spread over Europe, western Asia and northern Africa. From Israel these authors report the occurrence of a diploid form (2n=14), D. glomerata L. ssp. judaica Stebbins et D. Zoh., in the Jerusalem and Safad areas and the presence of a tetraploid form (2n=28) in several other localities throughout Israel.

For several polyploid groups the general outlines of the distribution areas of the various diploid and polyploid forms have been already worked out. This is also true for the *Dactylis glomerata* polyploid complex (Stebbins and D. Zohary 1958). However, in cytogeographical studies published on polyploids and polyis little or no information concerning spatial relationships of diploids and polyploids in areas where they come in contact. Since there are indications that gene flow from diploids to tetraploids might occur in contact areas (D. Zohary and Nur,

^{*} Part of this work is included in a M.Sc. Thesis submitted by the first author to The Hebrew University of Jerusalem.

in press), a knowledge of the nature of such contacts can add to our understanding of the genetic relationships between diploids and polyploids. It can also contribute to a better evaluation of ecological differences between chromosomal levels.

In the present work an attempt was made to study intensively a small segment of the general distribution area of the *Dactylis* complex, with the aim of finding out the details of the distribution patterns and relationships between the diploid and tetraploid forms.

MATERIALS AND METHODS

The survey of the geographical distribution of the diploid and tetraploid forms of *Dactylis* was carried out roughly in two stages. In the early part of the work about 50 samples of *Dactylis* were taken from various parts of the Mediterranean territory of Israel and examined as to their chromosome numbers. Stations were relatively widely spaced and represented the main soil types and plant communities in which *Dactylis* is to be found in Israel. Later, the authors concentrated their work on areas where diploid populations were found. Mapping was based only on cytological examination. From each station, usually two plants were examined.

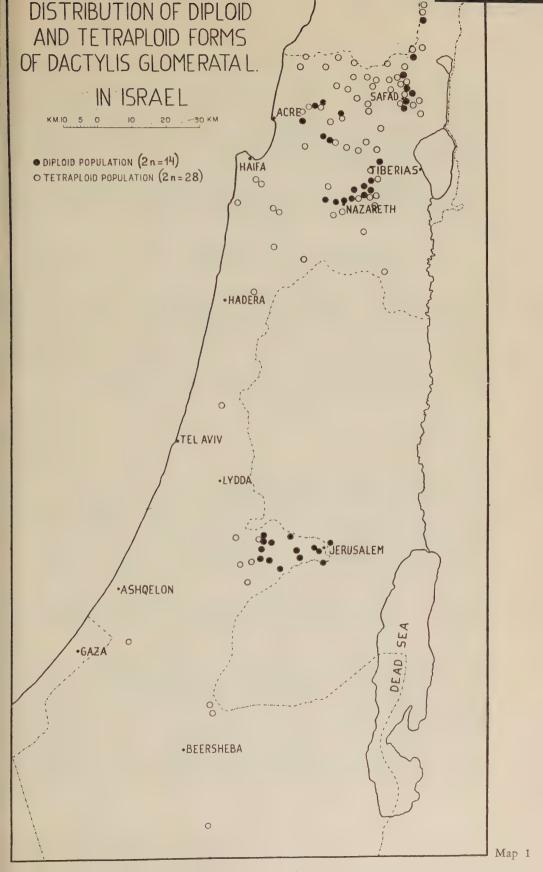
For cytological study, material was fixed in 3:1 alcohol acetic acid for 24 hours and stored in 70 per cent alcohol. The acetocarmine squash method was employed. Chromosome counts were made from microsporocytes during season. Growing shoots were dissected longitudinally and pretreated before fixation with an aqueous solution of paradichlorbenzene for three hours.

For ecological orientation, reference should be made to the publications of M. Zohary (1947a, 1947b) and to the geological maps of Picard (1957) and Shiftan (1952).

GENERAL FEATURES OF THE DISTRIBUTION OF DIPLOIDS AND TETRAPLOIDS

The results of the cytogeographical survey are presented in Maps 1 and 2. A total of 150 stations were examined.

Diploid Dactylis was found to occupy the following areas in Israel (see Map 1): a) the main ridge of the Judaean Hills in the Jerusalem Corridor, b) the hilly area around Nazareth, c) the Safad area in Upper Galilee, d) several additional smaller stations in various places in western and northern Galilee. A striking feature of the distribution of the diploids is their occurrence as small enclaves or as clusters of patches within a territory occupied by the tetraploid plants. Ecologically, most of these areas are characterized by typical Mediterranean dwarf shrub ("batha") associations in which Poterium spinosum is dominant. They receive no less than 550 mm annual rainfall. Edaphically, diploid plants were found to be confined to terra-rossa and light rendzina soils derived from limestone, chalks and marls of the Cretaceous and Eocene formations.



Tetraploid *Dactylis* is spread over most of the Mediterranean territory of Israe (see Map 1). In contrast to diploids, tetraploids are common also in some semi steppe plant formations which border the Mediterranean region, where the annuar rainfall does not exceed 300 mm. Isolated stands of tetraploids penetrate ever further into the desert (e.g. Wadi Migra south of Beersheba), where these plants occupy especially favourable niches. While diploids have been found to be confined to calcareous soils, tetraploids occur also on red sandy loams, kurkar sand stone, dark rendzinas, basalt soils and loess. These data indicate that the range of ecological adaptation of tetraploid *Dactylis* is apparently much wider than that of the diploid and almost completely overlaps with the latter.

SPATIAL RELATIONSHIPS AND ECOLOGICAL DIFFERENCES BETWEEN DIPLOIDS AND TETRAPLOIDS

The three main areas in which diploids occur in Israel (Jerusalem, Nazareth and Safad), have been examined as to the spatial relationships between diploids and tetraploids. An attempt was also made to determine the ecological differences between adjacent diploid and tetraploid populations. The three areas were found to differ from one another in their ecology and their distribution patterns. It was therefore felt necessary to describe the situation in each area separately.

a) Judaean Hills

Diploid plants were found to be continuously spread over the main ridge of the Judaean Hills in the Jerusalem Corridor. Here this chromosomal form is a consistent component of the *Poterium spinosum* dwarf shrub formation (M. Zohary 1947a) which dominates this area. Diploid *Dactylis* plants grow on terra rossa soil derived from Cenomanian dolomites and hard limestones as well as on light rendzinas originating from chalks and marls of the Senonian and middle Cenomanian. Throughout this area it was noticed that *Dactylis* plants were more common on marly or chalky bedrocks and on slopes facing north.

It was possible to delimit the extension of the diploid form in this area only on the west. Diploids do not occur in the foothills of the Judaean Hills and were found only at altitudes above 400 metres. On the main ridge, diploids most probably extend north and south beyond the Israel borders.

Tetraploids were found to occupy the lower, warmer foothills west of the main ridge (see Map 1), usually at elevations not exceeding 300 metres.

In the area of Hartuv — Shaar Hagai, no direct contact could be found between the two chromosomal forms. They are separated here by a gap one to four kilometres wide.

In conclusion, it seems that in the Judaean Hills diploids are restricted to higher altitudes, while tetraploids are found in lower altitudes.

b) Nazareth area

Diploids occupy the higher parts of the hilly region around Nazareth at altitudes ranging from 250 to 550 metres and are associated mainly with *Poterium spinosum*. They grow on terra-rossa soil, on hard limestones of the middle Eocene as well as on a variety of light rendzinas derived from chalks and marks of the Senonian and Eocene periods.

The "diploid territory" around Nazareth seems completely surrounded by tetraploids which were found to replace the diploids at lower elevations. Tetraploids are also found at comparatively high elevations (e.g. Mount Tabor, elev. 588 m), where the bedrock is Cenomanian hard limestone.

No interruption has been observed in the distribution of *Dactylis* plants in the western and eastern parts of the Nazareth area. Since diploids were found in higher places and tetraploids in lower places, one can safely conclude that diploids and tetraploids come in contact here over considerable distances. One contact zone, two kilometres west of Beit Keshet, was examined, and the replacement of diploids by tetraploids was found to be quite sudden, the zone of mixed populations being only about a hundred metres wide.

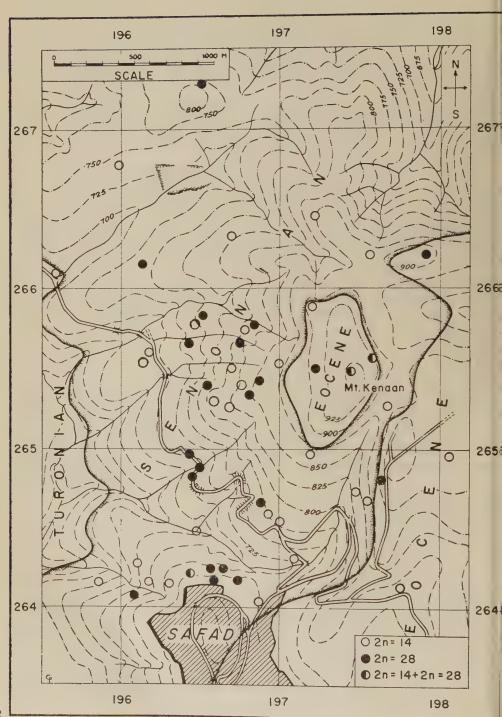
In conclusion, diploids are restricted to the higher parts of this hilly area also in the Nazareth area. However, in contrast with the Jerusalem area, diploids do not grow here on Cenomanian hard limestones. They are, instead, restricted to Senonian and Eocene bedrocks.

c) Safad area

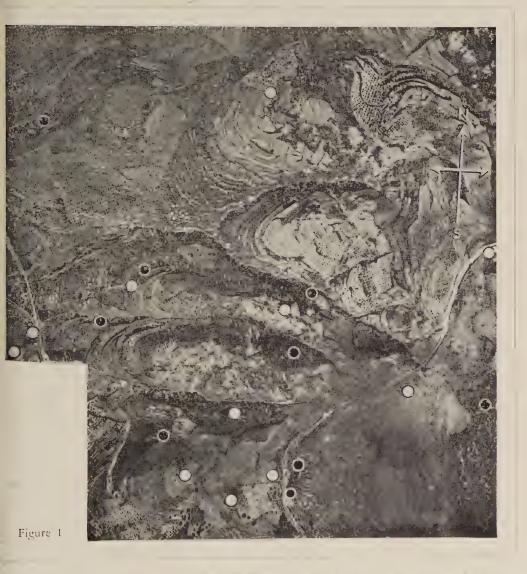
Dactylis plants are densely and continuously spread over the hilly area of Safad and Mount Kenaan. In contrast to the relatively large continuous areas of diploid populations around Jerusalem and Nazareth, diploids around Safad form a considerable number of small islands within a "tetraploid territory" (see Maps 1 and 2). East and west of this area no diploids were encountered. In the semi-steppe shrub formation towards the East and in the Mediterranean associations of Poterium spinosum on Cenomanian bedrock, towards the West, only tetraploids were found.

In this area diploids were found to occupy two main types of soils: 1) light rendzinas on Senonian chalks and marls, and 2) terra-rossa on hard Eocene limestones.

On the soft Senonian bedrocks, diploids occur on the steep, northfacing slopes in association with a dense cover of *Poterium spinosum* (see Map 2 and Figure 1). On the same bedrock, tetraploids occupy the ridges and slopes facing south, where the *Poterium* cover is usually much sparser. These differences in ecological preferences are most pronounced on the western side of Mount Kenaan, which is deeply cut by several wadis running from east to west. The topography here provides conditions for alternating strips, only a few hundred metres wide, of diploid and tetraploid plants (see Figure 1 and Map 2).



Map 2



Vertical airphoto (scale 1:10,000) of the western slopes of Mount Kenaan, near Safad. The steep, north facing slopes, with the dense cover of *Poterium spinosum*, appear as dark strips. Full and hollow circles represent diploid and tetraploid stations respectively.

On hard Eocene limestone, which is characterized by the *Ononis natrix* association, diploids were found only in the higher parts of Mount Kenaan (elevations 900 metres and more). They occur here on the ridges themselves as well as on adjacent slopes but are replaced by tetraploids in the lower parts of the slopes.

In conclusion, at least elevation, exposure and bedrock are involved in determining the distribution patterns of diploids and tetraploids around Safad.

The territory around Safad should be regarded as a large area of contact between diploids and tetraploids. *Dactylis* plants are continuously spread over the entire area, and due to the mosaic distribution pattern found (diploids and tetraploids replace each other every several hundred metres!), contacts between the two chromosomal forms must be common. Three such contact areas (see Map 2) were studied in some detail — one on the northern outskirts of Safad, a second 300 metres further east and a third on the top of Mount Kenaan.

In the first location, tetraploids were found on a south-facing slope, while diploids occupied a north facing slope. A mixed population of both chromosomal forms was found in a narrow belt, about 100 metres wide, on a slope facing northwest. As expected, three triploid plants were detected by checking plants for male sterility (non dehiscent anthers) and later by cytological examination. In the second and third contact areas five additional triploids were detected. A study of these natural triploids and their progeny is described elsewhere (D. Zohary and Nur, in press).

DISCUSSION

The data obtained indicate that the local diploid form, *D. glomerata* ssp. *judaica*, is restricted to true, relatively humid Mediterranean conditions, while tetraploids grow both in Mediterranean and in more arid, semi-steppe habitats. These differences manifest themselves also in areas where the two forms occur side by side. In such areas diploids show a preference to north-facing slopes, higher elevations and marly bedrocks — factors which apparently determine more favourable water conditions. The fact that tetraploids penetrate into drier habitats is in accordance with the conclusion previously reached on morphological grounds (D. Zohary 1956). Two diploid forms, the local *D. glomerata* ssp. *judaica* and the Iranian *D. glomerata* ssp. *woronowii* contributed their genes to the formation of the East Mediterranean tetraploid level. It is apparently the genetic contribution from the steppe form *D. glomerata* ssp. *woronowii* that has enabled the tetraploid populations to occupy the more arid habitats in Israel.

Another point that should be stressed concerns methods employed in cytogeographical studies. Distribution areas in such studies are usually based on chromosome counts taken from samples collected widely apart. It is believed that the distribution patterns found in the Safad area are not confined to this place or to Dactylis alone and that similar patterns exist also in other groups. In studies based on geographically widely spaced samples, one is apt to overlook certain forms altogether and may also be led to erroneous conclusions as to the distribution of the forms studied.

It is in many cases difficult to evaluate the differences in ecological requirements of diploids and polyploids from samples taken widely apart. The habitats of such samples usually differ in many ecological factors, and the presence of many variables naturally complicates the analysis. In the present study comparisons of habitats of adjacent diploid and tetraploid populations considerably helped in the understanding of the differences in the ecological requirements of the two forms. Comparisons of adjacent habitats are simpler and therefore safer. They can add critical information to the knowledge of the ecology of each chromosomal form and should be carried out whenever possible.

The comparatively sharp boundaries between diploid and tetraploid territories with only narrow transitional belts of mixed populations are significant. While in many cases changes in ecological factors are apparently gradual, changes in populations are quite abrupt. These facts indicate that each chromosomal form has its own adaptive niche and that the presence of diploids or tetraploids in any given area depends upon a delicately balanced equilibrium between each chromosomal form and the environment as well as between the diploids and the tetraploids themselves. This is also suggested by the very fact that small enclaves of diploids succeed in maintaining themselves even when completely surrounded by tetraploids.

Another fact, which might have important evolutionary bearing, is the occurrence of numerous contacts between diploid and tetraploid populations. If the sterility barriers between diploids and tetraploids are incomplete, favourable spatial conditions for gene-flow occur here. The possibility of such gene-flow is discussed elsewhere (D. Zohary and Nur, in press).

Throughout this study it was repeatedly observed that the range of morphological variation of tetraploid plants considerably overlaps with that of the diploids. Thus it was found impossible to separate a diploid plant from a tetraploid one on a morphological basis. These observations support the view expressed by Stebbins and D. Zohary (in press) that diploid and tetraploid forms in this group should be regarded only as subspecies of the same species complex.

ACKNOWLEDGEMENTS

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XYLEM STRUCTURE AND ANNUAL RHYTHM OF DEVELOPMENT IN TREES AND SHRUBS OF THE DESERT II. ACACIA TORTILIS AND A. RADDIANA

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ABSTRACT

The wood anatomy and annual rhythm of development, as well as the seasonal changes of starch content in Acacia tortilis (Forsk.) Hayne and A. raddiana Savi were examined and described. The wood is diffuse-porous and the growth rings indistinct. Vessels are solitary or in multiples of 2-3 (-4) or in large clusters. Intervascular vestured pits were observed in both species. Wood parenchyma forms concentric bands which are broader in A. raddiana. Rays are homogeneous. Fibre walls include inner gelatinous layers.

The cambium was found to remain active throughout the year in both species examined. A prominent starch-free zone in the periphery of the xylem could be

observed only when the cambium exhibited a very strong activity.

The present article on two species of Acacia, A. tortilis (Forsk.) Hayne and A. raddiana Savi, growing in the Southern Negev (mean annual rainfall 25 mm), is the second of the series (Fahn 1958). These species grow in wadis and profit from the run off water from the adjoining catchment area. Both trees are Sudano-Deccanian elements growing in their main area of distribution in the savannah formation.

MATERIALS AND METHODS

Material examined was taken from the trees growing in Wadi Fukra, approximately 5 km west of the southern end of the Dead Sea. The two specimens of Acacia tortilis, trees No. 33 and 36, had trunks 45 and 35 cm in diameter respectively. The specimens of A. raddiana were numbered 34 and 35, and their respective girths were 30 and 70 cm.

Chips of the outermost wood were removed with a chisel at about chest height. Samples were taken monthly during the period 2 November, 1954 — 26 October, 1955, as well as on several later occasions. Twigs were also examined. Methods of chip sampling, staining procedure, slide preparation and examination are as

those described in the first article of the series (Fahn 1958).

ACACIA TORTILIS

Wood anatomy (Figures 1, 3, 4)

The wood was found to be diffuse-porous and growth rings indistinct, especially in the trunks. The vessels are mostly solitary but also occur in radially, diagonally and even tangentially oriented multiples. The number of vessels in the multiples is usually 2-3 (-4). Irregular clusters of a larger number of vessels were also observed. Sometimes the cluster consists of one broad and several narrow or very narrow vessels. The maximum tangential diameter of the vessels measured was 250 µ. Perforations are simple and may be transverse or oblique. Vessel member length was found to be from 60 to 300 (to 400) μ . Also present are vessels with tailed ends. Intervascular pitting is generally alternate, and the pits are medium-sized with linear aperture. Contrary to Chudnoff (1956), vestured pits were observed. Tyloses were not found but gum-like masses were present in the vessels. Wood parenchyma is paratracheal of the aliform- confluent type and forms narrow concentric bands. Long vertical strands of cells containing rhomboidal crystals occur frequently. These strands were observed to be more abundant in regions differentiated during the period of weak cambial activity. Large starch grains were found in all the wood parenchyma cells.

The rays are essentially homogeneous and mostly multiseriate, from 8 to 60 cells high, but short uniseriate rays, even only one cell high, are also present. The number of rays per millimetre was found to be between 3 and 6. Ray cells store starch but to a lesser extent than the parenchyma. The tangential diameter of the ray cells is generally $10-20\mu$.

Fibres 0.7 - 1.4 mm long have very thick walls with inner gelatinous layers (Figure 5) and few simple pits.

Rhythm of cambial activity

Examination of slides prepared from sample of A. tortilis, collected on successive: months, indicated that the cambium is active throughout the year (Table I). The

TABLE I

Intensity of cambial activity in Acacia tortilis

(The figures represent the number of outermost layers of xylem cells with incompletely thickened walls)

Num- ber of speci- men-	2 Nov. 1954	8 Dec. 1954	5 Jan. 1955	Feb.	16 March 1955	April	13 May 1955	17 June 1955	18 July 1955	21 Aug. 1955	23 Sept. 1955	2¢ O# 19)
33	4-12	±10	6-10		2-4	17–23	10–16	6-8	±10	10-20	±10	±
36	3-4	3-4	2-3	2-3	2-4	2-4	2–4	6-8	6-8	8-10	5-8	3

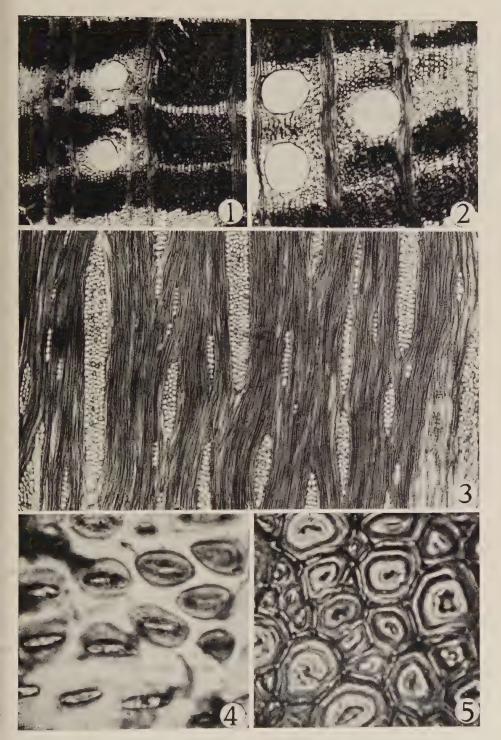


Figure 1. Acacia tortilis, cross-section of wood. × 52. Figure 2. A. raddiana. cross-section of wood. × 52. Figure 3. Acacia tortilis, tangential section of wood. × 80. Figure 4. A. tortilis, intervascular vestured pits. × 1850. Figure 5. A. raddiana. cross-section of wood, showing fibres with inner gelatinous layers. × 820.

samples from the stem of specimen 33 showed weak cambial activity in March 1955, and in specimen 36 a low rate of cambial activity throughout the year, except during the period June to September, was established. Cambial activity of twigs from specimen 33 was weak to medium during the months January - July but relatively strong from August to December. In specimen 36 such strong late-season activity was confined to the months September - November.

Seasonal changes in starch content

Examination of sections treated with I₂KI from the successive monthly samples taken from the more active tree, i.e. specimen 33, revealed the presence of a prominent starch-free zone in the outermost xylem during the months May - October. In specimen 36 no such prominent zone could be observed throughout the year. During periods of relatively high cambial activity, starch grains were lacking only in the recently formed xylem tissue. The differences between the two trees can be explained by the fact that in tree 33, during the period of high cambial activity, relatively more xylem cells were produced than in tree 36. This resulted, in tree 33, in the mobilization of a larger amount of carbohydrates.

Phenology

Flowering started at the end of May, and flowers could be seen on the trees till the end of July. Shoot and leaf development seemed to be continuous throughout the year, althoug not always simultaneously on all the branches of the tree. This continuous development is comparable to the duration of the cambial activity.

ACACIA RADDIANA

Wood anatomy (Figures 2, 5)

A detailed description of the wood structure of *Acacia raddiana* trees growing in Fezzan (N. Afr.) is given by Messeri (1938). The wood elements of our specimens differ from those described by her, mainly by larger dimensions. The wood structure of the trees examined by us was found to be similar to that of *A. tortilis*, except for the following differences:

- 1) The aliform-confluent wood parenchyma forms broader concentric bands.
- 2) In the region of the parenchyma bands, the rays are wider, i.e. up to 12 cells wide.
- 3) The number of rays is smaller, i.e. 3 4 per millimetre. Ray cells are 10- 25μ in tangential diameter.
 - 4) Fibre length is 1.0 1.7 mm.

Rhythm of cambial activity

Here, as in A. tortilis, the cambium remained active throughout he year (Table II). Tree 35, the more vigorous specimen, showed high cambial activity in almost

TABLE II

Intensity of cambial activity in Acacia raddiana
(The figures represent the number of outermost layers of xylem cells with incompletely thickened walls)

Num- ber of speci- men	Nov.	8 Dec. 1954	Jan.	Feb.	March	April	May	June	July	21 Aug. 1955	23 Sept. 1955	26 Oct. 1955
34	±6	1-3	1–2	2-4	2–4	2–3	2–4	±3	5-7	2-4	2-4	3–6
35	±10	±10	±8	_	>10	±20	10-15	5-10	±10	5	>20	±10

all of the samples examined. Tree 34, the weaker specimen, showed low cambial activity in the trunk during December and January. In the same months the stem of tree 35 showed quite prominent growth of the xylem, so much so that in a later sample, taken on the 6th December 1955, 30 - 40 rows of unthickened xylem cells could be counted. The cambium in twigs was also active throughout the year, while no clearly perceptible fluctuations in the annual cambial rhythm could be recorded.

Seasonal changes in starch content

Starch grains were abundant throughout the wood parenchyma and rays, reaching in most cases quite or almost the cambium. However, in samples exhibiting very high cambial activity, grains were absent from the two outermost concentric parenchyma bands.

Phenology

Flower heads appear at the beginning of July and continue to develop until the beginning of December. In analogy to A. tortilis, the shoot and leaf development is continuous throughout the year.

DISCUSSION

A close similarity exists in the wood structure of A. tortilis and A. raddiana, the only main distinguishing feature being the broader concentric bands of aliform-confluent wood parenchyma in A. raddiana.

In both species the cambium remains active throughout the year. This behaviour is similar to that of the three species of *Tamarix* described in the first article of this series (Fahn 1958). This supports the view, that the temperature of the Negev does not exert a limiting effect on the cambium activity. It is continuous, provided sufficient water is present.

Both Acacia species grow in regions with an extremely low rainfall limited only to a short winter period, and are confined there to wadi beds. Their roots

penetrate into deep soil layers and even during the late summer months are able to obtain sufficient water accumulating from the surrounding hills.

The annual changes in starch content of the xylem are less prominent than in *Tamarix* spp. (Fahn 1958) where the width of the srtach-free zone is closely correlated to changes in cambial activity. However, even in the *Acacia* species studied a prominent starch-free region in the peripheral xylem could be observed in periods in which the cambium showed a relatively very high activity.

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CITRUS GERMINATION AND EMERGENCE AS INFLUENCED BY TEMPERATURE AND SEED TREATMENTS *

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ABSTRACT

Germination and emergence of sour orange seeds were tested at five different temperatures; seeds presoaked in water, were germinated in Petri-dishes. Germinating media were: tap water (for untreated seeds and for seeds dipped into powdered charcoal) and soak water (for untreated seeds). Other seeds of the same species were germinated in containers at different temperatures and depths.

The optimum for the rate of germination was found at or near 26°C. The presence of inhibiting substances in the soak water was confirmed. Soak water did not delay citrus germination but reduced fungal attack in dishes. Charcoal delayed germination and prevented fungal attack. Both the rate and the ultimate percent-

age of emergence were negatively correlated with depth.

The effects of temperature and previous treatments on germination and emergence of citrus seeds have received in the past only scarce attention (Fawcett 1929, Camp et al. 1933, Elze 1949). In the present paper some additional information is reported on the above and related topics.

MATERIALS AND METHODS

Rubidoux sour orange seeds removed from fruits (kindly supplied by the Department of Horticulture, University of California, Citrus Experiment Station, Riverside, California and picked on January 13, 1956) were thoroughly washed, soaked in water for 22 hours at room temperature and sown in Petri-dishes 15 cm in diameter, padded with two layers of No. 5 Watman filter paper. Four replicate dishes containing 50 seeds each were sown on January 19 for each treatment.

^{*} This investigation has been carried out at the Earhart Plant Research Laboratory, California Institute of Technology, Pasadena, during the tenure of a Research Fellowship, between December 1955 and April 1956. The author gratefully acknowledges helpful suggestions by Dr. F. W. Went and the facilities provided by the laboratory and its staff.

Treatments were: 5 different constant temperatures in darkness (17°, 20°, 23°, 26°, 30° C) and 3 different treatments of seeds a) germination in soak water (each ml containing material eluted from 5 seeds), b) germination in tapwater, c) germination in water after coating of seeds by dipping them into powdered charcoal ("Nuchar"). The amount of water or solution added initially to every dish was 25 ml, while the paper was kept moist by adding water whenever needed.

The soak water was tested to assess the presence of inhibiting substances by means of wheat seeds (4 replicate samples of 100 seeds of the Salkirk variety). The length of wheat roots developed at 17° C after 64 hours was evaluated by a five degree scale and compared to water control, in a way similar to that used by Cohen (1956). The soak water was tested for acidity and found to contain 6 mg eq. of acidity per litre.

On February 13, additional seeds were extracted from fruits of the same lot, which had been stored in the meantime at room temperature. After thorough washing, 25 seeds were sown in each of 32 small square plastic containers filled with a 1:1 mixture of medium vermiculite and small gravel.

Seeds were sown at 2 cm depth in four replicate containers for each of the above temperatures, while four replicate containers were also sown at the following depths: 1, 3, 4 cm and kept at 26° C. Careful irrigation was supplied according to needs, and containers were kept in darkness.

A seed was considered germinating when a protruding root tip was visible. Emergence was judged by the first emerging of seedlings from soil. In the second case more than one emerging stem per seed may be counted, due to polyembryony of seeds (about 4% of seeds growing in containers originated more than one seedling).

Results of germination and emergence experiments were calculated in percentages and in number of days required for germination or emergence of 50% of the seeds which eventually germinated or emerged (see Cohen 1956).

A certain amount of mould infestation could not be prevented, notwithstanding the initial desinfection of seeds; this is not unexpected in germination tests lasting up to two months and more.

RESULTS

The average elongation of wheat roots grown in soak water was significantly lower (at the .01 level) than that of roots grown in tap water: 292 vs. 342 (sum of grades multiplied by their frequency in every dish which contains 100 seeds). The inhibiting substances present in the soak water (which induce in wheat roots an inhibition of about 15% as compared with water control) do not influence the speed of germination of sour orange seeds, as shown in Table I.

TABLE I

Days required for germination of 50% of germinating sour orange seeds at different temperatures and with different treatments

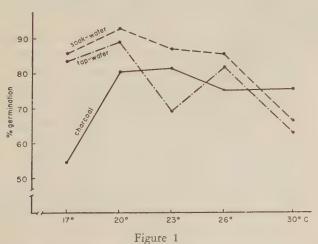
Temperature (°C)							
Treatments	170	200	230	26°	300	Average	
Soak water	50.0	39.0	29.2	25.3	- 26.2	33.9	
Water	54.2	37.0	31.0	23.7	26.0	34.4	
Charcoal	64.0	47.0	37.2	28.0	26.0	40.4	
Average	56.1	41.0	32.5	25.7	26.1		

Statistical analysis

Temperature effects	F = 202 **
Treatment effects	F = 27 **
Interaction: temperature × treatments	F = 3.8 **
Soak water + water vs. charcoal	F = 54 **
Soak water vs. water	F = 0.2, N.S.

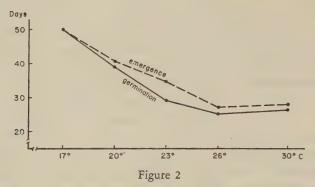
Germination was considerably delayed by charcoal, the more the lower the temperature of germination. The difference in days (from average of soak water and water) was +11.9, +9.0, +7.1, +3.5, —0.1 at 17°, 20°, 23°, 26° and 30°C respectively.

The ultimate germination percentage is lower in tap water than in soak water, due probably to higher incidence of fungal attack (especially at 23°C where two tap water dishes were heavily infested) which was apparently hindered by soak water (see Figure 1).



Ultimate percentage of germination at different temperatures and with different treatments.

In the case of 30°C fungi developed also in soak water, and only with the seeds coated by charcoal germination was over 75%. The germination percentage of charcoal-treated seeds at 17°C is due to incomplete germination at low temperature at the time when the experiment was discontinued on April 11 (83 days from sowing).



Number of days required for 50% germination in soak water and emergence from depth of 2 cm at different temperatures.

In Figure 2 the number of days required for the *emergence* of 50% of the seedlings is compared with the number of days required for the *germination* of 50% of seeds germinating in soak water, at the same temperatures. The difference is surprisingly small. The soak water treatment of the germination experiment has been used in this comparison, for the following reason. The seeds of the emergence experiment had not been soaked before sowing. If any substances influencing germination should be eluted from seeds by irrigation water, the vermiculite which forms their seed-bed will adsorb at least part of them and they may be able to act as the substances found in the soak water.

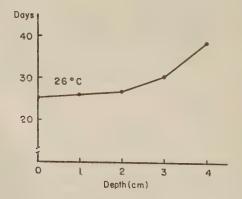


Figure 3

Number of days required for 50% emergence from different depths of sowing at 26° C.

The fact that the emergence experiment was sown a few weeks after the germination experiment should not be overlooked. The seeds remained thus longer in the fruit.

According to Elze (1949), emergence should have been delayed and not hastened by storage of seeds in the fruit.

The effect of greater depth on the rate of emergence was considerable (Figure 3). Depth also affected final emergence percentages at 26°: 87%, 82%, 74% and 60% for 1, 2, 3 and 4 cm respectively.

From Figure 2 it also appears that the Q_{10} of the rate of germination and emergence in sour orange seeds is about 2 in the range between 17° and 27° C, i.e. at temperatures below the optimum or near it.

DISCUSSION

The optimum temperature for germination of sour orange seeds, found in our experiments in the neighbourhood of 26° C is in accordance with the findings of Fawcett (1929) who, however, had good results also at 23° and at 29°. Somewhat higher optima were found by Camp et al. (1933).

The optimum depth for emergence seems to be rather small, as already stated by Elze (1949) who found delay in emergence even at 2.5 cm. In our experiments, both speed and ultimate percentage are best when seeds are sown one cm deep or even less. Obviously the drying effect of solar radiation, renders a too shallow sowing dangerous and unadvisable from the practical standpoint.

Cohen (1956) has already stated the inhibiting effect of water, into which sour orange seeds had been soaked, on wheat roots and on stripped citrus seeds. He insisted on the rapid inactivation of the inhibitor preventing a delay in germination of intact citrus seeds, a process, which requires quite a long time.

Although our results cannot be directly compared with Cohen's, both the presence of inhibitors and their lack of effect on germination of intact citrus seeds have been confirmed. It is interesting to note that apart from inhibiting growth of wheat roots, soak water has also a fungistatic effect. The acidity of 6 mg eq. per litre of soak water possibly due to citric or malic acids present in citrus juice, could explain the effect on wheat growth (Prill et al. 1949). On the other hand, Heinemann and Engels (1954) have shown that organic acids, and citric acid amongst them, have an inhibiting effect on the growth of certain fungi at concentrations ranging between 3 and 6 mg eq. per litre.

Charcoal both delayed germination and reduced fungal attack. From Elze's (1949) tables we learn that in 7 out of 9 experiments, germination of seeds previously stored in charcoal was somewhat delayed as compared with germination of seeds previously stored in sand. The mechanism responsible for delay is not yet understood. Delay of germination and fungistatic effect may be partially responsible for satisfactory results obtained when shipping citrus seeds in charcoal over long distances.

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CAUSES OF RAPID WILTING OF CUT DAHLIAS AND MEANS TO IMPROVE THEIR KEEPING QUALITIES

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ABSTRACT

Cut dahlias have a rather short keeping life, corresponding to a relatively short life of inflorescences blooming naturally on the mother plant. Two days after picking, uptake of water is hampered by plugs originating in the xylem vessels.

Bacterial infections, affecting keeping qualities adversely, are not of primary importance, since antibiotics increase keeping time only by about one day. Treatments reducing respiration rate, as dipping stems in maleic hydrazide (50 p.p.m.) increase keeping time by about the same period.

MATERIALS AND METHODS

Two varieties of dahlias were used throughout this investigation (while other varieties were occasionally tested):

- 1. "Tel Aviv". A yellow-red local variety belonging to the "Formal Decorative" class with a head 11-14 cm in diameter.
- 2. "Rosy Pink". A medium purple-pink variety belonging to the "Miniature Decorative" class with a head 8-9 cm in diameter.

The dahlias were picked in the morning and transferred to jars each containing 300 cc of different solutions of preservative substances (six replicates).

Wilting proceeds centripetally. A scale of 6 progressive degrees was used. "1" designating incipient wilting of only the external row of ray florets, "6" complete wilting and brown discoloration of the whole head. Intermediate degrees symbolize progressive wilting, coupled with loss of turgor and colour.

Sections of stems were examined for bacteria by the "Claudius" method (Schneider and Zimmermann 1922). The "Gram" method (Johansen 1940) was used for their preliminary classification. The daily changes in weight of excised flower heads and the amount of water absorbed through their stem were determined. A few analyses of CO₂ output by inflorescences were carried out with a slightly modified apparatus of Heinicke (Heinicke and Hoffmann 1933).

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RESULTS

Influence of preservative chemicals on rate of wilting

Water controls attained degree "3" of the wilting scale about 4-5 days after picking, and differences between varieties and preservative solutions were slight (\pm one day).

A slight improvement in keeping qualities was obtained by immersion of stems into warm water (50°C) and by use of "Chrysal" (a commercial flower preservative — by Pokon at Naarden, Holland), while very hot water treatment (100°C) often recommended and popular with house-wives, was found detrimental.

Wilting of dahlias unsevered from the mother plant

Comparing wilting of cut dahlias with that of unsevered flowerheads, it was found that the latter remained only for about two more days in marketable condition. Floral 'life' of dahlias is therefore short even under natural conditions.

Bacteria and their control

Bacteria are found only on the cuts of picked still fresh-looking dahlias. In wilting flowers kept in water for several days, they can be found in all internal tissues of the submerged stem, especially around xylem and phloem bundles. Their number increases as wilting progresses.

To control bacterial growth, antibiotics were used. Penicillin-procain and streptomycin were used as aqueous solutions, dissolving 120,000 units in 300 ml of water, while penicillin was smeared as a paste (1000 units per gram) on the stem.

In both varieties streptomycin retarded wilting by about one or two days, the difference against water controls being highly significant. Both penicillin solution and paste had a lesser effect, but retarted wilting at least in one of the two above-mentioned varieties. The streptomycin treatment controlled bacterial growth almost completely during seven days, and even wilted inflorescences did not show appreciable amounts of bacteria. It should be noted that this antibiotic controls both Gram positive and Gram negative bacteria.

Inhibition of respiration

Assuming that wilting is at least in part a consequence of depletion of assimilates, it was tried to delay it by slowing down respiration and other katabolic processes. The following solutions of growth regulators were tried: 2,4 - D (5 and 20 p.p.m.), ethyl phenyl carbamate (3 p.p.m.), maleic-hydrazide (MH: 50 and 200 p.p.m.). Dahlias were kept with their stems in the above solutions. While the 2,4-D treatments increased the rate of wilting, as expected, and the carbamate treatment did not differ from control, the MH treatment was found to delay wilt-

ing. The 50 p.p.m. solution significantly delayed wilting of both varieties, the 200 p.p.m. only of the Rosy Pink variety (Figure 1).

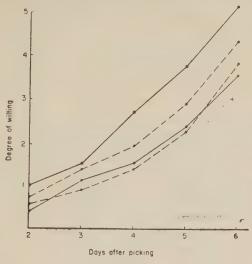


Figure 1

Since M.H. treatments reduced the rate of wilting, a few respiration measurements were carried out with flower heads kept in solutions of 50 p.p.m. M H Table I shows much larger output of carbon dioxide by flower heads kept in water than in M H While output in water increased with time, it decreased in M H solution. In contrast, 2,4-D has been found to increase respiration of plants, especially in low concentrations (Kelly and Avery Jr. 1949).

TABLE I

Average carbon dioxide output (mg/hr) of comparable

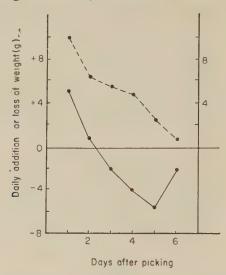
dahlia's heads kept in water and in 50 p.p.m. maleic hydrazide

	After 1 day	After 3 days
Water control	8.9	10.1
50 p.p.m. M.H.	6.2	5.5

Water relations and plugging of vessels

Figure 2 shows daily changes in weight and water absorption by dahlia inflorescences of the Tel Aviv variety when kept in water for a few days. Similar trends were found with the variety Rosy - Pink. There is a trend towards a decrease in both processes during 6 days from cutting. An increment in weight has been established during the first 48 hours, but later on, the weight of inflorescences decreases

as compared with initial weight. At the same time, water absorption decrease from about 10 ml during the first day, to less than 1 ml during the sixth.



Daily addition or loss of weight (g, •———•) of cut dahlias (Tel Aviv variety) and their daily absorption of water (ml, •——•—•)

The initial increase in weight seems to be linked with initial uptake of water; filling up a saturation deficit, while later on, weight decreases because of transpiration and to a lesser extent, as a consequence of respiration. One of the reasons for decreased water uptake seems to be obstruction of vessels by brown plugs which can be seen in transverse section, especially in the vicinity of the basal cut. They seem to originate from disintegrated cellular material, and could not be analysed. On the other hand the relatively small number of thyloses found could hardly explain the reduction of water uptake in contrast to assumptions by Molischi (1888).

ACKNOWLEDGEMENTS

This work is an abridged version of a M.Sc. thesis. The author wishes to express her thanks to Prof. H. R. Oppenheimer and to Dr. S. P. Monselise for guidance during the investigation and for preparing the present English text.

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BACTERIAL SOFT ROT OF AVOCADO FRUIT. II.

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ABSTRACT

A bacterial soft rot disease on avocado fruit was found in Israel for the first time in December 1953. The causal organism was identified as *Erwinia carotovora* var. aroideae. Like other organisms of the same group it is a wound parasite and re-

quires relatively high humidity to induce infection.

The pathogenicity of the organism to 4 different varieties of avocado fruits and to several other hosts was tested. It produces lesions similar to those of the original avocado fruits on all 4 varieties. It induces soft rot in tomato and pepper fruits as well as on slices of potato or carrot in the presence of water. On potato plants it causes typical black leg symptoms, followed by collapse, and disintegration of the stems.

Other tested isolates of *E. carotovora* var. *aroideae* as well as of *E. atroseptica* induce lesions similar to those produced by the avodado isolate on avocado and other hosts. The pathogenicity temperature range of the avocado isolate is wider, however. Infection spreads more rapidly at higher than at lower temperature. The optimal temperature for infection is 30–32°C; very good infection is produced at 36–37°C, and good, though slow infection is induced at 14°C. No infection occurs above 38 or below 12°C.

The close relationship of the avocado organism and other isolates of *E. caroto-vora* var. *aroideae* with *E. atroseptica*, the causal organism of the black leg disease of potatoes, is discussed.

A bacterial soft-rot disease in avocado fruits was found in Israel for the first time in December 1953 on several fruits picked from a single tree of the California Variety H. L. The disease was caused by an organism belonging to the soft-rot group of bacteria originally identified as *Erwinia aroideae* (Townsend) Holland (Bergey et al. 1948) and later by Rudd Jones, Dowson and others as a non-gasforming strain of *Bacterium carotovorum* (L. R. Jones) Lehman et Neumann (Rudd Jones 1950), or *Erwinia carotovora* (Jones) Holland (Bergey et al. 1948) or *Pectobacterium carotovorum* (Jones) Waldee (Dowson 1957). This organism was not yet mentioned in the literature in connection with avocado. It was finally identified as *Erwinia carotovora* var. *avoideae* or *Pectobacterium carotovorum* var. *aroideae* (Dowson 1957). A short account of the disease and its cause has been given cisewhere (Volcani 1954).

In this paper the results of further experiments comprising the pathogenicity of the organism to 4 different winter varieties of avocado fruits (Fuerte, Annaheim, Nabal and Benik), to tomato and pepper fruits and to potato plants are described. The results of infection experiments on avocado fruits of the Nabal variety with 2

other isolates* of E. carotovora var. aroideae and 2 isolates** of E. atroseptica (var. Hall) Jennison (Bergey et al. 1948) are also reported. Finally, the close relationship of the avocado organism with isolates of E. atroseptica is discussed.

Healthy unripe detached fruits were inoculated either by pricking through drops of sterile distilled water suspension of 48 hours old slant cultures, or by spraying with the same suspension without pricking. The inoculated fruits and controls were kept in bell-jars over water or without water at temperatures of 12, 14, 20. 25, 30-32, 36-37 and 38°C.

Healthy potato plants grown in pots were inoculated on their stems by the methods described above, and kept in the incubator under bell-jars overnight at 25°C. They were then put outdoors, and the bell-jars were removed. Temperatures ranged from 14-16°C during the night to 20-30°C during the day.

Positive results were obtained only with material which had been pricked through drops of the suspension of the organism. Infection experiments with reisolations from lesions gave similar results. Microscopic examination of Gramstained affected tissues of inoculated specimens revealed numerous Gram-negative rod-shaped bacteria. The organisms recovered from the lesions of inoculated hosts were identical with the respective original isolations.

All tested organisms required relatively high humidity to produce infection. Progress of infection was more rapid at temperatures of 30-37°C for the avocado and pepper isolate, than at 25 and 20°C, and attained its maximum rate for the former isolate at 30-32°C. No infection was produced at below 20°C with the pepper isolate, but good, though slow infection was produced at 14°C with the avocado isolate. The progress of infection for the tobacco isolate and the 2 isolates of E. atroseptica was greater at 25 than at 20 and 32°C; no infection was produced at 36-37°C.

Infection was produced on all four varieties of the avocado fruits inoculated with the avocado isolate, and there were no significant differences in the sizes of the lesions. The lesions were similar to those observed in the original fruits except with the Benik variety. They appeared as soft dark flat spots around centres of infection (Figure 1). Eight or nine days after inoculation at 32°C, the spots coalesced and covered the entire unripe fruits. In longitudinal section of inoculated fruits, the infected tissue appeared softer than the healthy and light to dark brown in colour. Sunken concave dark-brown pits often appeared under the skin around the centre of inoculation (Figure 2). A putrid smell evolved from all infected fruits.

On unripe Benik fruits the lesions appeared at first as dark spots quite distinct from the green healthy skin. But as soon as this fruit starts to soften, it normally

tato isolate received from Dr. Dowson.

^{*} No. 37 isolated from pepper fruits in Israel (Volcani 1953a); No. 66 isolated from tobacco in Uganda, received from Dr. W. J. Dowson, Cambridge, England. ** No. 74 isolated from potato stem in Israel (Volcani 1953b); No. 274 an American po-

darkens, and it was therefore impossible to distinguish between the healthy and diseased area. When the fruit was cut, however, the diseased tissue under the skin showed lesions similar to those described above.

Lesions similar to those produced by the avocado isolate appeared on the Nabal fruits inoculated with the 2 isolates of *E. carotovora* var. aroideae, and the 2 isolates of *E. atroseptica*. The progress of infection was greater, however, with the avocado isolate than with the four other organisms at their respective optimal temperatures.

Lesions on tomato and pepper fruits as well as on potato and carrot slices were similar for all 5 organisms. Inoculated green tomato and pepper fruits showed light to dark-brown, soft, flat spots around centre of inoculation (Figure 3). Following inoculation at 25°C, the spots coalesced and a soft rot of the entire fruit ensued after 3–4 days with the avocado organism, and after 5–8 days with the others. The skin of the tomato fruits was often raised and shrivelled, and deep cracks developed in the infected area (Figure 4). Ripe tomato fruits were affected with soft-rot to the same extent as the green fruits. Inoculated potato and carrot slices in water developed solt rot of the parenchyma.

Distinct signs of black leg similar to those produced by the *E. atroseptica* isolates appeared within 24 hours on potato plants inoculated with the avocado organism. The inoculation-wounds had developed into elongated dark brown to black lesions, and brown streaks appeared on the stems (Figure 5). The upper inoculations developed more rapidly than did the basal. The basal lesions appeared within 3 days after inoculation, but wilting of the leaves followed by collapse of the stems and disintegration ensued 3–4 days later.

The avocado isolate has also been found to be closely related in many of its biochemical activities as well as in its pathological characteristics with the black leg organism *Evwinia atroseptica*; it differs only in its maximum and optimum growth and pathogenicity temperatures which are higher.

These results are in agreement with the author's preliminary findings and with Hellmers's and Dowson's experiments showing that various isolates of potato black leg and soft rot bacteria produce similar effects when inoculated into the vascular bundles of potato plants (Hellmers and Dowson 1953). Furthermore, another strain of *E. carotovora* var. aroideae more recently isolated from maize plants (Volcani 1958) was also found to cause typical black leg symptoms when inoculated on stems of potato plants.

These results emphasize once more the conclusion of Hellmers and Dowson contrary to Burkholder and Smith (1949), that the group of organisms identified as *E. atroseptica* are strains or varietics of the group of the soft rot organisms identified in Bergey as *E. carotovora* (Jones) Holland (Bergey et al. 1948), which Hellmers and Dowson preferred to term *Bacterium carotovorum* (L. R. Jones) Lehman et Neumann (Hellmers and Dowson 1953) and lately as *Pectobacterium carotovorum* var. atrosepticum (Dowson 1957).

Experiments have shown that the avocado organism is not specific to the H. L. Californian variety, but is capable of infecting other winter varieties of avocado fruits. Since its maximum pathogenicity temperature is above 37°C, it is likely that the organism can infect summer varieties of fruits under favourable humidity conditions.

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Figure 1
noculated unripe Nabal avocado fruit showing soft,
dark flat spots around the centre of infection.



Figure 3

Inoculated pepper fruit showing soft, flat, brown spots.



Figure 4

Inoculated tomato fruit showing soft, flat, light brown, cracked spots.



Figure 2

Inoculated Annaheim avoca fruit showing sunken conca dark brown pits under the sl around centre of infection.



Figure 5
Inoculated potato plants show typical black leg symptoms days after inoculation. The of the stems in the upper oculations are bent over, wi and turned black. The basal oculations show dark brielongated lesions and long bristreaks developing along stems upwards from the wor

ENDURANCE OF A DROUGHT PERIOD BEYOND THE WILTING POINT

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INTRODUCTION

According to Meyer and Anderson (1952), drought resistance is "the capacity to survive periods of drought with little or no injury". Many tree species occur in arid zones where they are subjected to long dry periods. The question arises whether these are true drought resistant species in the above sense and in the sense of Parker (1956), or whether they have some source of available soil moisture and evade drought instead of enduring it.

By adapting Bourdeau's (1954) method, the ability of the following plants to survive prolonged drought periods with the soil moisture below wilting point was tested. The merit of this method lies in using for examination entire plants instead of detached organs. Furthermore, with water deficits rising beyond the wilting point, also desiccation resistance (Levitt 1956) is considered. *Desiccation resistance* is defined by Iljin (1931) as the ability of plant tissue to endure dehydration, and is often related to properties of the protoplasm (primäre Dürreresistenz of Arvidsson 1951, or plasmatische Dürreresistenz of Stocker 1956).

EXPERIMENTAL

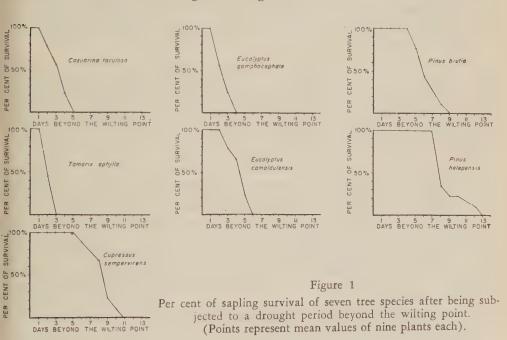
The most common Israel afforestation trees were chosen for the following experiment: Tamarix aphylla (L.) Karst., Eucalyptus gomphocephala DC., E. camaldulensis Dehn, Casuarina torulosa Dry., Cupressus sempervirens L., Pinus halepensis Mill., P. brutia Ten. The ability of five of the above species to grow under the arid conditions of the Negev was summarized by Zohary and Waisel (1956).

Cuttings of *Tamarix aphylla* and one-year old saplings of the other species tested were planted in glass jars containing 600 grams of sandy-loam soil. The plants were grown in the greenhouse for one month, after which they showed well developed roots. Two sunflower plants were then sown in each jar and left to grow until they had three pairs of leaves. Irrigation was subsequently withheld. In each jar in which permanent wilting of sunflower plants occurred the latter were removed, and the jar — now containing the tree sapling only — was placed inside a thermostat where temperature (20°C), light intensity (300 f.c.) and relative hu-

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midity (55%) were kept constant. The experiments were conducted during the winter, when the plants showed no or very slow growth. The period during which each jar was to remain inside the thermostat varied from one to thirteen days for the different plants.

After each sapling had undergone its planned period of drought, the jar was watered and returned to the greenhouse. Attention was paid during the following weeks to the appearance of new roots and shoots, this being accepted as the criterion of survival. Results are given in Figure 1.



DISCUSSION

Although the above method seemed to be promising for laboratory determination of drought resistance, no clear correlation between the survival of the various plants and their respective habitats or their behaviour in the field was found. Of the two species of pine examined, *Pinus halepensis*, the species better suited to dry habitats, also better endured the experimental drought period. Similar results were obtained with the two species of *Eucalyptus*, *E. camaldulensis* being more resistant than *E. gomphocephala*. On the other hand, the experimental results both of *Cupressus*, a true Mediterranean species, and of *Tamarix*, a species with a typical Saharo–Sindian distribution, were in obvious contradiction to what might be expected of these plants in view of their occurrence in nature. *Cupressus*, though evincing a high resistance in the laboratory test, fails under arid conditions in the field. On the other hand, the desert tree *Tamarix aphylla* was the least resistant species in our experiment, thus corroborating our suggestion, which

will be expressed elsewhere, that T. aphylla is of a humid tropical origin, and even in deserts grows in localities with ample reserves of stored underground water.

The high drought resistance of Cupressus and Pinus might be connected, among other properties, with their relatively slow growth, with the high ability of water retention in their shoots (cf. Parker 1951), or with their low transpiration during water shortage (Oppenheimer 1932, 1947). The relatively fast-growing and high-transpiring species — Tamarix, Eucalyptus and Casuarina — show a tendency towards being less resistant to prolonged drought periods. Tamarix and Eucalyptus seem to evade drought in the field owing to their steadily fastgrowing roots, since their relatively high transpiration values offer no indication of water shortage.

The above findings call for further investigation along these lines.

ACKNOWLEDGEMENTS

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NOTES

The calcium and magnesium content of germinating lettuce seeds

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Little is known about the mineral constituents of lettuce seeds and the changes occurring in them during germination. Mayer (1954) has investigated some of the heavy metals occurring in these seeds. In the present investigation the calcium and magnesium content of the seeds was determined at various stages of germination. In addition, distribution of these elements in various fractions of the seeds was determined.

Lettuce seeds, variety Grand Rapids, were used throughout the experiment. Lots of 250 mg were germinated in Petri dishes with 3–5 ml water at 26°C in the dark. After two hours in the dark, they were given a light stimulus of about 250 f.c. for 3–5 minutes to improve germination. After various periods of time the whole seedlings were harvested and ashed, or the seedlings were homogenized, fractionated and the fractions ashed. The fractionation was effected as follows: The whole seeds or seedlings were ground in a mortar with water and the resultant homogenate centrifuged at 1000 g for 10 minutes. Thus the water soluble and water insoluble fractions were obtained.

These fractions were further separated as follows: Alcohol was added to the water soluble fraction up to a final concentration of 50% and the solution heated in a water bath for 10–12 minutes. This precipitated a fraction which contained chiefly proteins. The soluble non-protein fraction contained ionic loosely bound calcium and magnesium and soluble organic calcium and magnesium compounds, while the "protein" fraction contained chiefly protein but possibly also a certain amount of pectins which are precipitated by the alcohol treatment. The water-insoluble fraction was extracted with petroleum ether to remove lipids. The residue was extracted with 10% NaCl for half an hour, resulting in a NaCl soluble and a NaCl insoluble fraction. The NaCl soluble one consisted primarily of globulin, and the NaCl insoluble one contained reserve protein and other structural components such as cell wall fragments. All the fractions were dried and then dry ashed.

The ashes were analysed for calcium and magnesium. Calcium was determined flame-photometrically after removal of phosphate on an amberlite column according to the method of Hemmingway (1956). Combined calcium and magnesium was determined by the EDTA titration of Smith and McCallum (1956). Magnesium was calculated as the difference between the total calcium + magnesium and calcium alone.

The results of these analyses are represented in Figures 1, 2 and 3. Every point in the graphs is a mean of nine determinations from three germination experiments. As is seen from the graphs, the total calcium content of the seeds does not change during germination. The total magnesium content shows a drop after 24 hours of germination. Expressed on a mg basis, therefore, the seeds clearly contain a much larger amount of calcium than magnesium. This is in accord with the results of Wallace (1954) on citrus but differs from those of Cooper et al. (1947). It is of interest to note, however, that on a molar basis the amounts of calcium and magnesium are roughly equal (The ratio Ca: Mg is approximately 11:10).

A survey of the limited data available in literature on the changes of the calcium and magnesium content of various seeds during germination does not show any clear relation between the content of these two elements.

From the results reported here it appears that in the total water soluble fraction, magnesium reached a maximum after 48 hours — declining later on. Calcium almost does not change at all (Figure 1). The calcium and magnesium content of water soluble non-protein fraction rises steadily with increasing time of germination, showing a clear tendency for both calcium and magnesium to become increasingly soluble as germination proceeds (Figure 2).

In the soluble protein fraction, magnesium reaches a maximum after 24 hours while the corresponding maximum for calcium is reached only after 48 hours (Figure 2). These changes may be considered in parallel with the sequence of mitosis and growth. In lettuce seeds mitosis begins after about 10–16 hours (Evenari et al., 1957), while growth processes proper begin at a later stage. The changes in the solubility of magnesium and calcium might be related to respective needs of the cells for these stubstances in mitosis and in growth.

The NaCl soluble fraction again shows a clear rise in magnesium content in the course of the first 24 hours of germination, while the rise in calcium content is not so pronounced (Figure 3). The NaCl insoluble fraction on the other hand shows a steady decrease in magnesium content while calcium shows a peak at 48 hours (Figure 3).

It is difficult to relate any of these changes to definite metabolic processes. The original water insoluble calcium and magnesium can be ascribed to phytin (Mayer 1958) which is present in sufficient amounts to bind large amounts of calcium and magnesium. As phytin breaks down the calcium and magnesium liberated are distributed among the various fractions.

The changes in the calcium and magnesium content differ considerably in the time of their occurrence. They evidently are utilized at different stages of the germination process.

The changes taking place between 48–72 hours of germination may be interpreted, but 72 hours old seedlings grown in the dark and pure water cannot be considered normal, as under normal conditions such seedlings would certainly be expected to absorb minerals from their environment, and to lead an autotrophic life. In the Petri dishes they no doubt will be suffering from starvation and any interpretation given to changes occurring in such seedlings will be unsuitable if adapted to normal plants.

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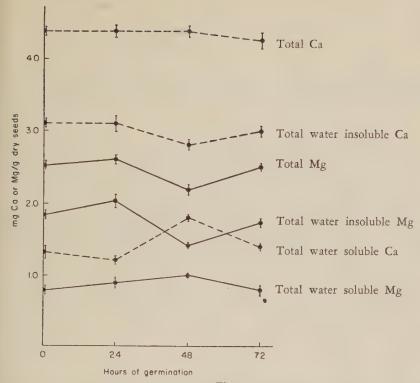
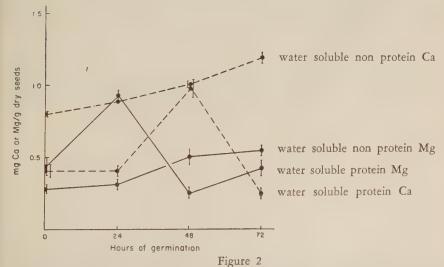


Figure 1
The changes in total, water soluble and water insoluble Ca and Mg during the germination of lettuce seed.



The changes in water soluble protein and non-protein Ca and Mg during the germination of lettuce seed.

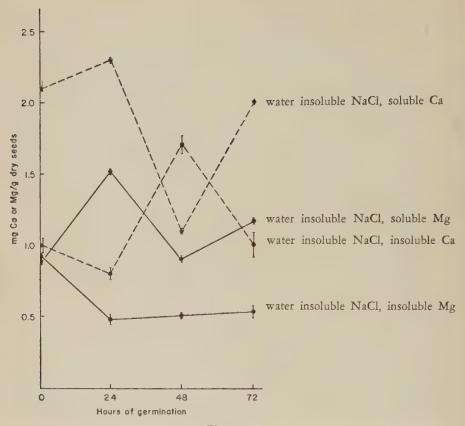


Figure 3
Changes in NaCl soluble and insoluble Ca and Mg in germinating lettuce seed.

Native types of Oryzopsis miliacea (L.) Asch. et Schw. in Israel*

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Three types of *Oryzopsis miliacea*, indigenous to Israel, are distinguished on the basis of morphological, phenological and ecological differences: a) a xerophytic Negev type, b) an erect northern grey-seeded type, and c) a semiprostrate northern brown-seeded type.

The differential features between these types are given in the following Table.

The northern brown-seeded type appears to be highly calciphilous and capable of establishing itself under extremely difficult conditions, e.g. on enbankments of recently prepared roadways, consisting almost exclusively of soft limestone. This type seems to be most suitable for pasture purposes and is adapted to highly calcareous soils in the Mediterranean territory. Both northern types grow here together. No transitional forms are found.

The Negev type is more variable and in several places (Sde-Boker, Tel Yeruham), forms occur with a more prostrate habit, broader leaves and darker seeds than the common Negev type; these forms resemble the northern brown-seeded type in many respects.

Varieties of this species from Morocco, Cyprus and California (Smilo Grass), grown at

Neve-Ya'ar, seem to be morphologically intermediate between both northern types.

Johnson (1945) in his detailed cytotaxonomic study on Oryzopsis, does not distinguish

between the various types.

Combination by breeding of the good forage properties of the northern brown-seeded type and the drought resistant Negev type could result in a very useful pasture plant, well suited to dry and poor habitats, where the establishment of other perennial grasses, such as *Phalaris tuberosa*, were so far unsuccessful.

A genecological study, concerned with the significance of the lime-tolerance of the brown-seeded type, as an example of an edapho-ecotypic response to the selective action of a single environmental factor (Gregor 1957, Kruckeberg 1951), was started recently.

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^{*} Publication of the Agricultural Research Station, Rehovot, 1957 Ser. No. 194-E.

Seeds Colour Lemma Caryopsis Wrinkling	Panicles Habit Length (cm) Whorls Ramification of panicles	Leaves Arrangement Breadth Length of basal leaves (cm) Length-of upper leaves (cm) Sheaths	Growth habit Height of flowering plants (cm)	Phenology Start of winter growth Tillering Flowering Seed ripening and drying off	Typical babitat	Place of collection
Grey Membranous, transparent Pale reddish-brown Coarse and irregular	Dense, narrow 45 ± 10 10 ± 3, close Non-branching, dense, short- pedicelled spikelets	Single leaf from each node So Narrow $(6 \pm 2 \text{ mm})$ 60 ± 10 40 ± 10 Stout, narrow	Erect, leafy, stout culms	Early, before first rains (15–30.IX) Very late (end April) Very late (mid-May) Slow and late (June–July)	mel, Lehavot Habashan Dwarf-shrub batha, brush and open maquis; in shade of olive, carob and pine plantations; hedges; dry wadis.	Northern grey-seeded type Neve-Ya'ar, Matsuba, Mt. Car-
Brown Brown and opaque Bright brown with dark furrow Fine, concentric, regular	Open, loose and short 30 ± 10 7 ± 1, open Branching, with 1–3 sub- branches and few spikelets on each	Sometimes 3–5 leaves from each node Broad to very broad (12 ± 3 mm) 40 ± 10 20 ± 10 Broad,delicate, marked in dry plants	Semi-prostrate, very leafy, delicate culms	Early, before first rains (15–30.IX) Late (mid-April) Late (begin, May) Slow and late (June–July)	Hasollelim, Kefar Hahoresh, Beit Govrin, Tsuba Mainly dwarf-shrub batha and open brush; roadsides; fields. Only on chalky marl and soft limestone, not on terra rossa.	Northern brown-seeded type Matsuba, Mt. Carmel, Tiv'on,
Pale brown (transitional forms darker) Pale brown, opaque Bright brown with dark furrow Fine, concentric, regular	Very open, loose 50 ± 10 10 ± 2 open Strongly branching, 1–4 sub- branches, few long-pedicelled spikelets on each	Always single leaf from each node Very narrow (5 ± 2 mm — transitional forms broader) 35 ± 10 3 ± 10 Stout, narrow (transitional forms broader)	Erect, xeromorphous, very stout culms	Late, after first rains Early (begin, April) Early (mid-April) Quick and early (May)	Natural springs and wells north of Kurnub and Wadi Ramon. In loessy and gravelly wadis and roadsides.	Negev type Kurnub, Sde Boker, Tel Yeruham

Growth and development of lettuce germinated in gibberellic acid

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Moore (1958) has recently described the effect of gibberellic acid on dwarf pea seedlings when applied to the seed. He showed that the gibberellic acid applied to the seed considerably affected subsequent growth, partially abolishing dwarfness. This is not the case for lettuce. The effect of gibberellic acid in the germination of lettuce has been previously reported (Lona 1956, Evenari et al. 1958). The subsequent growth and development of lettuce was followed. Lettuce seeds variety Grand Rapids were germinated in a solution of gibberellic acid 10 mg% for 48 hours in the dark. The seedlings were then transplanted to pots kept in a greenhouse. The hypocotyls of the treated seedlings were considerably longer than those of the untreated controls (Figure 1). However, gibberellic acid treatment during germination in no way effected elongation of the subsequent internodes, the plants developing into normal lettuce plants. Both controls and treated plants were bedded out and their further development was observed. Treated and non-treated plants showed similar development and flowered at the same time.

In other experiments, gibberellic acid was applied daily directly to the terminal bud of lettuce seedlings. These treated plants elongated markedly as long as the treatment was continued. Leaves were small and narrow. The whole plant had an etiolated appearance (Figure 2). As soon as treatment was discontinued, elongation ceased. The newly formed internodes were short, the leaves were more normal in appearance and development of a head could be observed (Figure 3). Renewal of treatment resulted in flower formation (Figure 3). Flowers had not yet developed on the controls when the experiments were discontinued (See Figure 3).

It seems that in lettuce gibberellic acid only affects the internodes directly treated. Prolonged application is required to cause such an effect, single applications or seed treatment being almost ineffective. The prolonged treatment also results in earlier flower formation.

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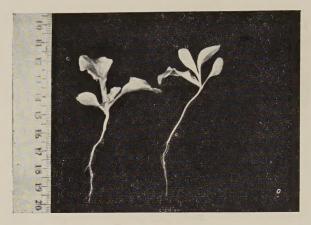


Figure 1
Lettuce seedlings germinated in 10 mg% gibberellic acid (right) or water (left) for 48 hours and then transplanted.



Figure 2
Lettuce plants treated with gibberellic acid (left) and controls (right).



Figure 3
The same plants as in figure 2
after cessation and renewal of
gibberellic acid treatment.

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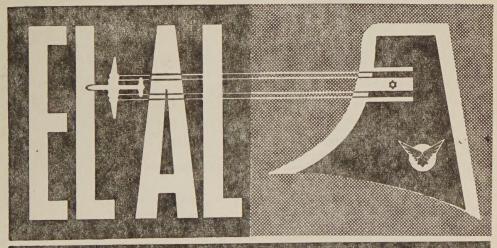
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